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# CONTINUOUS AND DISCONTINUOUS VARIATIONS AND THEIR INHERITANCE IN PEROMYSCUS

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## I. INTRODUCTION

MANY of the views which we are now accustomed to associate with the names of Weismann, Bateson, DeVries, Nilsson-Ehle and others were either foreshadowed or clearly formulated by Francis Galton, many years earlier. Galton's polygon, by which he illustrated the difference between continuous and discontinuous variations, is doubtless known to most readers; as is also his distinction between "blended" and "particulate" inheritance. It is less familiar, perhaps, that Galton regarded all inheritance as "largely, if not wholly, 'particulate.'" Even skin color, the classic example of blended inheritance in man, is presumably "none the less 'particulate' in its origin, but the result may be regarded as a fine mosaic too minute for its elements to be distinguished in a general view." Again, "the blending in stature is due to its being the aggregate of the quasi-independent inheritances of many separate parts" (1889, p. 139).

Galton did not deny all heritability to those variations which were represented by the minor oscillations of his polygon, although he refers to such variations as "unstable."

With the modern revival of Mendel's principles of

heredity and the definite formulation of a "mutation theory" of evolution, some of Galton's more or less tentative views have crystallized into dogmas. Along with the two just mentioned, there has been incorporated the principle of the "continuity of the germ-plasm," a conception which was likewise first clearly formulated by the great English geneticist, though its modern expression we owe to Weismann.

These various hypotheses have been woven together into a single fabric and made to reinforce one another. It will hardly be denied that some rather flimsy reasoning has been employed at times by those here concerned. Thus one familiar syllogism runs somewhat as follows: Somatic modifications are not inherited; fluctuating variations are not inherited; therefore fluctuating variations are somatic modifications. Indeed, "somatic" and "non-hereditary" have come to be used interchangeably by many writers. Whether or not somatic modifications ever become germinal is a matter to be settled by evidence. But I must confess that I have never regarded as self-evident the contention that because characters are found to be "non-hereditary" they are, *ipso facto*, "somatic" in origin.

A certain sanctity and inviolability has come to be attached to the units of heredity or "genes," according to the neo-Mendelian creed. Not only do these units refrain from any degree of blending, but—save for occasional mysterious "mutations"—they are quantitatively and qualitatively unchangeable. Thus, the only differences upon which selection, natural or artificial, can act are differences due to the presence or absence of different genetic factors. "We know," say the Hagedoorns, in an article (1917) which is typical of much of the recent literature of heredity, "that all the different genes, all the different inherited factors . . . are each in themselves invariable. . . . Liability to change by selection is synonymous with genotypic variability, and this true variability is synonymous with impurity."

Much dialectic skill has been displayed in maintaining this set of opinions against the many facts which seem directly to refute them. Indeed, it must be conceded that a fairly consistent and logical edifice has been erected upon these foundations. Strictly logical, though oftentimes improbable interpretations have been given to each new volley of hostile data, until the fortress has begun to seem impregnable—at least to a frontal attack.

But perhaps, of late, another metaphor has come to suit the situation better—that of the two knights fighting on opposite sides of the same shield. The Mendelians have recently had recourse to more and more minute factorial differences in explaining certain lesser gradations of color in some of their material, until at length the distinction between their opponent's "continuity" and their own "discontinuity" is more imaginary than real. Water is a continuous medium for all the ordinary purposes of life, and solutions of different substances may be completely "blended" therein. Its resolution into hypothetical molecules, atoms, electrons and the like does not in the least affect these fundamental facts.

The publication of the data which I offer in the present paper confessedly does not constitute a "frontal attack" upon the multiple factor hypothesis. My results belong to a class of facts which have already figured extensively in this controversy, and which have been met by ingenious and plausible counter-arguments. As I have stated elsewhere, I am led to doubt very seriously whether any *conceivable* evidence could be brought forward which would be admitted by the more extreme neo-Mendelians to be really damaging to their position. As in so many other cases, the victory is to be won, if at all, through a process of "attrition." Positions are gradually abandoned which are never *disproved* in a logical sense. Indeed, as hinted, above, there are clear signs that the defenders of the "multiple factor" explanation of selection and blended inheritance are already retiring from their main positions.

## II. The Distribution of Subspecies

The term *subspecies,* as here employed, is nearly equivalent to *geographic race.* These subdivisions of a species occupy different, though often contiguous areas. When contiguous, they are said to intergrade completely with one another along the boundaries of their respective territories; and in any case, their ranges of variation overlap broadly. It is this fact, indeed, which leads to their being ranked as subspecies, rather than as distinct species, since the differences between some of the more widely separated among them would be quite sufficient to give them specific rank were there no connecting forms.

In such reports as those of Osgood on *Peromyscus* (1909), Nelson on the rabbits (1909), or Goldman on *Neotoma* (1910), the geographic ranges of certain species are seen to be divided up into what look like quite arbitrary subdivisions, corresponding to the ranges of the component subspecies. The boundaries between these subdivisions oftentimes follow certain natural barriers, but in some instances this does not appear to be true. And, in any case, it is doubtful whether any geographic barrier, save a continuous body of water or a lofty and unbroken range of mountains could prevent the free diffusion of such rodents. These minor areas, furthermore, frequently comprise territory having a very wide diversity of physical conditions. For example, *Peromyscus maniculatus gambeli* is represented as ranging from the foggy coastal area of central and southern California across the hot, semiarid San Joaquin Valley to the snowy heights of the Sierra Nevada. And in latitude, its range is said to extend roughly from the 31st to the 48th parallel.

According to Osgood,

> Specimens from Monterey, the type locality, are absolutely identical with those from San Diego and the northeast coast of Lower California, and the intervening region is inhabited by exactly the same form. These, moreover, are like specimens from . . . the west slope of the Sierra (p. 69).

We might well be puzzled to discover any common ele-

ments of the physical environment which were responsible for the presence of the same subspecies under such widely divergent conditions of life. Particularly is this true when the environmental differences, as in the present case, far exceed those between the habitats of certain quite distinct subspecies.

Nor does the contention seem justified that such extensity in the distribution of a single subspecies is fully accounted for by the absence of any insurmountable barriers to its dispersal. So far as geographic features are concerned, the barriers between the range of *gambeli* and the ranges of certain neighboring subspecies seem to be no greater than some of those which traverse the territory of *gambeli* itself. Looking at the distribution maps in such publications as those just mentioned, one is impressed by a seeming analogy between the boundaries of these various subspecific ranges and those of the political subdivisions of the earth's surface. In considerable degree these last are bounded by geographic features, but to a large extent, also, the lines of demarcation seem to be drawn quite arbitrarily—the territories merely bound one another.

While great weight must be given to the findings of these taxonomic experts, I think it is our duty at present to accept certain of their conclusions with considerable reservation. This is particularly true of assertions as to the *absolute identity* of the characters of specimens from widely different parts of a given range. The published data make it plain that the authors are in no position to detect minor differences of a statistical nature. A small number of specimens from each locality are commonly compared, the measurements "in the flesh" of the various specimens necessarily having been made by a number of different collectors. It will be evident from the ensuing pages that the differences with which we are dealing are often of such a nature as to be revealed only by the comparison of large numbers of individuals, measured according to uniform standards. As regards the

latter point, tests which I have made of the standards of measurement employed by several competent collectors show clearly that the differences due to "personal equation" are sometimes at least as great as those which characterize quite distinct local races.

Accordingly, we might feel justified *a priori* in entertaining some skepticism as to the homogeneity of these races of animals throughout such great areas. Furthermore, I already have a certain amount of direct evidence which renders this contention improbable. Such evidence will be considered later.

An extremely desirable undertaking would be to run a series of trapping stations through the territories of two

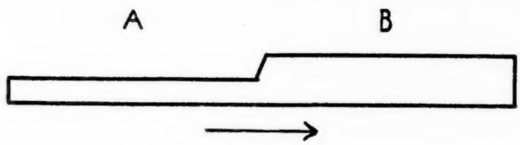


Fig. 1.

adjacent subspecies, at right angles to the supposed line of demarcation. This the author hopes to do in the course of time, though the task is not as simple as might perhaps be anticipated. Theoretically, a number of possible conditions might be revealed by such an investigation.

In the first place, it might be found (Fig. 1) that each of the two races was, in reality, "absolutely identical"

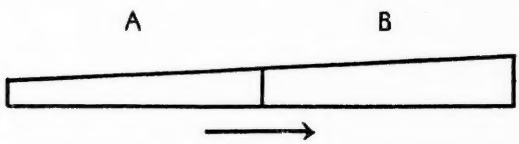


Fig. 2.

throughout its own range, while the transition between the two might be fairly abrupt.

Secondly, there might be an unbroken intergradation, in respect to the differential characters, throughout the

entire ranges of both the races (Fig. 2). In this case there would be no real boundary between the two groups, and indeed the recognition of two subspecies, rather than one or three, would be quite an arbitrary procedure.

Finally, there might be a condition, less easy to represent by diagrams, in which neither race was completely homogeneous, each being subject to considerable local variation within its own territory. Such local differences might or might not tend to be graduated as indicated in Fig. 2. Or, there might be some degree of gradation with respect to certain characters (*e. g.*, pigmentation), but not with respect to others (*e. g.*, length of appendages). In such circumstances, the recognition of two "subspecies" would depend upon the fact that the population of each of the respective territories was *relatively* uniform, and the changes encountered at the boundary *relatively* abrupt.

I am not yet in a position to say with certainty which of these possibilities is realized in the case of the species with which I am dealing (*Peromyscus maniculatus*), but I already have some strong evidence that the third one most nearly represents the actual state of arairs. As regards depth of pigmentation, we certainly find something approaching a graded series as we pass from the interior desert regions of California toward the coast, or as we pass from the coast of southern California, northward into successively more humid regions, as far as Alaska. But here we are dealing with a number of "subspecies." I have grounds for believing, however, that similar gradations occur within areas conventionally assigned to single subspecies.

Other questions of high theoretic importance relate to the nature of the animals inhabiting the so-called "areas of intergradation." Does this intermediate population manifest a complete blending of all the subspecific characters, or does it consist of a mixture of individuals, severally exhibiting the respective racial characters in a fairly pure state, or may there be a mosaic condition more

directly suggestive of Mendelian segregation? A definite answer to these questions I am likewise obliged to defer for the present.

Truly representative collections have been made by me thus far at only four stations within the State of California, though various other points have been visited and considerable numbers of the mice have been trapped there. My four principal collecting stations are located near Eureka, Berkeley, La Jolla and Victorville.[1] Meteorological records were kept for about two years at each of these points. These records have not thus far been carefully analyzed, however, so that their publication must be postponed. A preliminary comparison of climatic conditions at these four points has already been made (Sumner, 1915*a*). It will suffice, for present purposes, to state that, as regards both atmospheric humidity and rainfall, these stations rank (from highest to lowest) in the order given above, *i. e.*, Eureka, Berkeley, La Jolla and Victorville; while as regards mean annual temperature the reverse order holds.

The distribution of the three subspecies of *Peromyscus maniculatus*, recognized by Osgood as occurring within the limits of California, is represented in Fig. 3. It will be seen that one of my stations (Eureka) lies within the range of *rubidus*, another (Victorville) within the range of *sonoriensis*, while the other two (Berkeley and La Jolla) lie within the range attributed to *gambeli*.

In the ensuing pages, I am not in the least concerned with characterizing and defining those taxonomic groups which have been called *Peromyscus maniculatus gambeli*, *rubidus* and *sonoriensis*. I shall merely discuss the differences between (and within) four representative collections taken by me in widely separated and climatically different regions of the state. The question as to what "subspecies" a given mouse "belongs to" is for my purposes a distinctly minor consideration.

[1] Four other stations have been added since the present paper was written, but the data derived from these can not be included here.

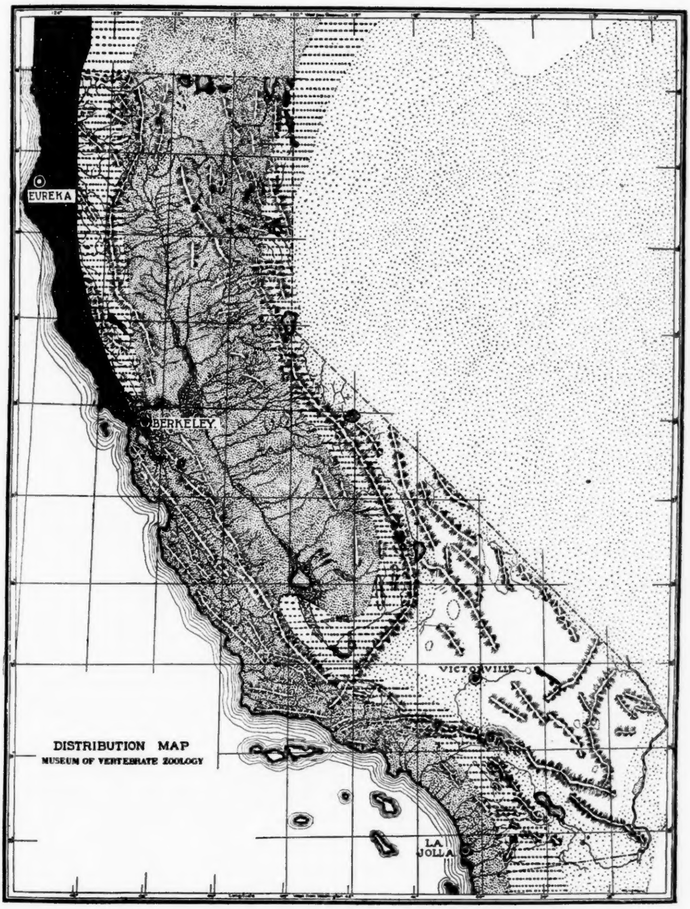


FIG. 3. Distribution of the recognized subspecies of *Peromyscus maniculatus* in California and Nevada, according to Osgood, 1909 (from Sumner, 1915). The heaviest shading denotes the range of *P. m. rubidus*, the intermediate shading that of *gambeli*, the lightest that of *sonoriensis*. Supposed areas of intergradation between two races are indicated by dotted lines.

## III. Differences between the Four Local Races under Consideration[2]

These differences may be divided, for the sake of convenience, into pigmental and structural ones. Since the former are the most obvious, they will be discussed first.

### 1. *Pigmental Differences*

The pigmental differences relate to (1) the hair, (2) the skin.

*Hair.*—Like the other members of the genus *Peromyscus,* the mice of the present group are covered with pigmented hairs upon the dorsal and lateral surfaces, while the ventral surface and to a large extent the feet are covered with white hair. Upon the trunk these white hairs are, to be sure, devoid of pigment only at the distal ends. Parting the pelage at any point, dorsal, ventral or lateral, reveals the presence of a slate-colored basal zone in each hair.

The most obvious differences between the races under consideration relate to the dorsal coat color (Fig. 4). This is darkest in the animals from the humid redwood district (Eureka), palest in those from the Mojave Desert (Victorville), and of an intermediate hue in the collections from Berkeley and La Jolla. These last two races likewise differ from one another, the former being darker than the latter. Thus we have a series of four gradations, which are correlated directly with gradations in the rainfall and atmospheric humidity of their respective habitats.

It is important to notice, however, that these differences of shade relate rather to averages than to individual cases. *All* of the Eureka mice are not darker than *all* of the Berkeley mice. Nor are all of the Berkeley mice darker than all of the La Jolla mice, nor all of the latter darker than all of those from Victorville. In comparing repre-

[2] I here use the word "race" as being a non-committal term, elastic enough to cover any two collections of individuals which show significant differences of type.

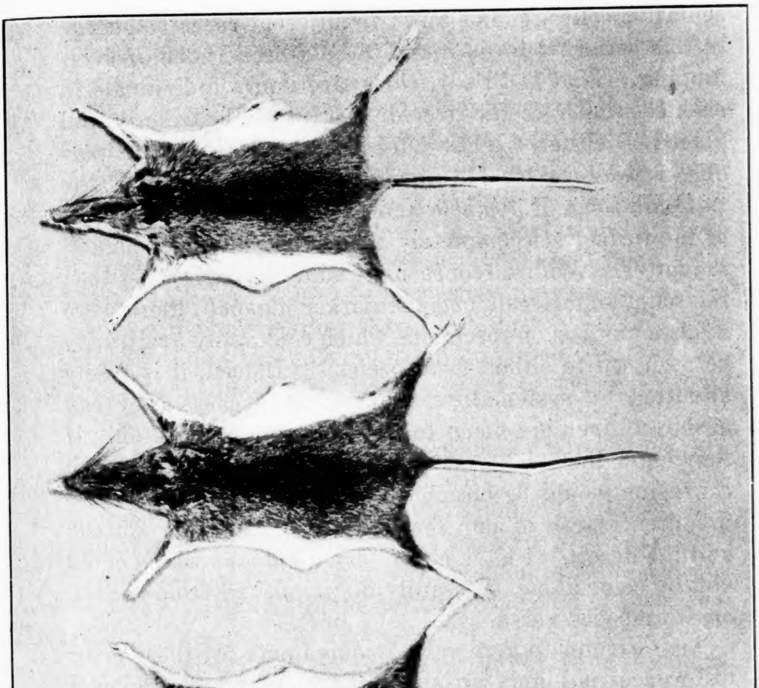

FIG. 4. Skins of male adult wild specimens of the Eureka, Berkeley, La Jolla and Victorville races of *Peromyscus maniculatus*, in order named. The skins have been selected with a view to showing the average shade of each series.

sentative collections of any two adjacent races belonging to this series, there is found to be a broad zone of overlapping. That is to say, there are many individuals in each set which, so far as color goes, could be equally well placed in either. I have, for example, laid out in parallel rows considerable numbers of *sonoriensis* and the La Jolla form of *gambeli*, and found that the darker half of the former set completely overlapped the paler half of the latter. While no confusion would be possible between the paler *sonoriensis* and the darker *gambeli*, there were a large number of specimens which could only arbitrarily be assigned to either "subspecies." Indeed, it is freely admitted by systematists that in many cases they can assign a given specimen to its proper subspecies only if they know the locality at which it was trapped. No such confusion would be possible, however, between the more divergent races of our series, *e. g.*, those from Eureka and the desert. I have never seen a *rubidus* which could not, by color alone, be readily distinguished from *sonoriensis* and vice versa.

Any attempt to give verbal equivalents for these color differences is highly unsatisfactory. In a later report I expect to undertake the analysis of these shades by means of a color wheel. For the present I will content myself with a very brief statement.[3] The dorsal darker stripe of the Eureka mice is of a shade lying somewhere between Ridgway's "sepia" and black, the paler lateral region lying between "Saccardo's umber" and "sepia."[4]

[3] The ensuing remarks apply only to the mature pelage. These mice pass through three distinct pelage phases: (1) the juvenal, which, in all races, is neutral gray in hue, and considerably darker than the adult shade; (2) the post-juvenal or adolescent, commonly paler and yellower than the last; (3) the mature or adult pelage, which is still more highly colored and frequently of still paler shade. The first molt occurs some time during the second month after birth, the second some time between the age of six months and a year. The various races of mice here considered, and even the mutants, are probably as clearly distinguishable in the immature pelages as they are in the adult.

[4] See Ridgway, 1912. "Dresden brown" and "mummy brown" perhaps approximate the shades in question as well as the last two mentioned.

Since the coat color is at no point homogeneous, any such comparison with uniformly tinted paper is of course very crude.

The desert mice are of a hue which can not even approximately be represented by reference to Ridgway's "color standards." The effect is probably not far from that which would result from a mixture of fine streaks of black and of "ochraceous buff" or "cinnamon buff," so proportioned as to approximate the general hue of the barren soil. As in all of these races, the mid-dorsal pelage is commonly darker than the lateral. All that need be said of the two collections of "*gambeli*" is that they are intermediate between the extreme types just referred to.

As a special case of the general hair color of the body, though not entirely correlated with this, is to be mentioned the color of the "ankle" region. The latter, particularly on its ectal surface, is covered with very short pigmented hairs, whose depth of shade affords another feature distinguishing the average condition of these four races.

I have given considerable attention to a microscopical examination of the hairs of these various mice. In position the pigment is of two different sorts, axial and superficial, located in the medulla and cortex respectively. A series of more or less disc-shaped, black pigment bodies extend from the base of each hair throughout the whole, or a considerable part, of its length. In the stouter hairs, there are, in the expanded region, two to four longitudinal rows of these bodies. In all cases, they alternate regularly with air spaces.

In the all-black hairs, the black pigment extends very nearly to the extreme tip. In the banded hairs, a region of varying length occurs in the distal half, in which the black pigment gives place to yellow. The dark pigment does not end abruptly, however. The dense black bodies become fragmented into their component rounded granules, as we pass from one segment to another, first giving

way to scattered collections of these granules (which are dark brown when seen singly) and later disappearing altogether. In the transitional region, black and yellow pigment may frequently be found in the same segment. In most hairs, the dark bodies again replace the yellow ones as we pass toward the tip; occasionally the yellow continues as far as any axial region is distinguishable.

The yellow pigment seems to be restricted to the axial part of the hair. To some extent, it occurs in the form of granules, but, unlike the black, it is largely present in a diffuse condition. This pigment is not all of the same tint, but varies in shade from a pale yellow to an orange or even a very pale brown.

For a varying length, on the distal, tapering ends of nearly all the hairs of the colored parts of the body, there is a very dark, granular pigment, lying close beneath the surface of the hair. This overlies and reinforces the axial pigment, so that the distal end is frequently darker than any other part of the hair. The superficial pigment, where dense, commonly looks almost black, but when seen in a thin layer the single granules appear brown. As already stated, this is likewise true, though in lesser degree, of the "black" axial pigment. In one of the "mutants," to be described later, this distal dark zone is nearly or quite lacking, and the same is true of certain exceptional samples of hair taken from normal individuals.

The yellow pigment is readily soluble in even fairly dilute potassium hydrate solutions, whereas the dark pigment is very much more resistant to this reagent, and may remain unchanged, even after the complete disintegration of the hair.[5]

Most students of this subject seem to follow Miss Durham (Bateson, 1903) in recognizing three pigments in the hair of *Mus musculus*—the black, the brown or chocolate, and the yellow. After considerable examination of the

[5] I have, however, observed preparations in which even the densest black pigment bodies assumed a reddish brown color, especially near the margin of the cover-glass.

hair both of *Mus* and *Peromyscus,* I can not feel sure of any sharp distinction between the black and the brown pigments. It is true that the axial pigment bodies of the basal portions of the hair are nearly dead black, while most of the superficial pigment at the distal ends is distinctly brown. But all gradations occur in the axial pigment of the transitional zones, and these gradations appear to be due not merely to differences in the density of the clusters of granules, but to gradations in the depth of color of the individual granules themselves. Without having made any careful chemical tests, I am disposed to believe that black and brown, in the hair of mice, are due merely to different degrees of aggregation of a single pigment. On the other hand, this dark pigment seems to differ, chemically and otherwise, from the various shades of yellow.

The differences in the color of mice of different subspecies and of different parts of the pelage of a single individual appear to be due to two chief causes: (1) the relative length of the pale zone, in relation to the rest of the hair; and (2) the proportionate numbers of the all-dark and of the banded hairs; probably also to (3) the depth of shade of the yellow pigment in the pale zones, and (4) the degree of concentration of the superficial pigment at the distal ends. In some of the "mutants," as will be pointed out below, certain other factors contribute to the differences shown.

Of importance for our general viewpoint is the fact that no one of the geographic races which has been examined possesses any type of hair which is wholly lacking in any other race. It would be impossible from a single hair, or even a small group of hairs, to say from what sort of mouse they were taken.

When viewed on the ventral side, these four races of mice likewise present characteristic differences. They form a graded series in respect to the whiteness of the pelage, which is purest in the desert race and least so in that from the redwoods. The differences are found to

result from the relative length of the terminal pigmentless zone which is present in these hairs. The ventral hair of the desert race also appears to be somewhat longer, or at least of a softer texture, than that of the others.

In the case of the ventral surface, like that of the dorsal, these differences relate to averages rather than to individuals. Likewise, it is of interest to note that within each race there is little or no correlation between the dorsal and the ventral shade. I have frequently graded a considerable row of mice of a single race in respect to the shade of the dorsal pelage, and found, on turning the animals over upon their backs,[6] that the order of arrangement did not correspond with the ventral gradations of shade.

Another differential character of these races is the degree of lateral extension of the ventral white area of the body, or, conversely stated, the ventral extension of the dorso-lateral pigmented area. The colored and uncolored regions of the body come together abruptly along an irregular lateral line extending from the snout to the tip of the tail. In the desert race, more of the white ventral region is usually to be seen in side view than is seen in the darker races. The gradation of the other three races among themselves is less obvious.

This degree of extension of the colored area relates not merely to the body but to the appendages. In the darker races an elongated tongue commonly extends down upon the fore-limb, in some cases even to the hand, while in *sonoriensis* such a ventral projection is usually little developed. The graduation of our four races in regard to this character corresponds to that noted in respect to shade. Similar conditions are observable on the hind limbs, particularly upon the ankle, where the pigmented hair may extend as far as the heel, or may fall short of this in varying degrees. The case of the tail will be discussed separately.

A hair character which seems to be peculiar to *sonoriensis,* among the races here considered, is the presence of

[6] Fresh specimens, not skins, are used for most of these comparisons.

small clusters of white-tipped hairs near the anterior insertions of the ears. But even this feature is not evident in all individuals.[6a]

Many species of *Peromyscus,* including the *maniculatus* series, have what is known as a "bicolored" tail. The hairs throughout a longitudinal stripe of varying width, upon the dorsal surface of this member are dark brown or black, while those of the ventral side are white. Now a casual inspection serves to show that this caudal stripe is broader and darker in the Eureka mice than in the desert ones, while a more careful comparison shows that the "*gambeli*" individuals are, on the whole, intermediate between the other two.

Fortunately, the breadth of this stripe is a character which may be subjected to fairly accurate measurement. It is my practice to slit the skin of the tail along the mid-ventral line, strip it off, and press the inner, damp surface firmly against a strip of black cardboard. The total width of this skin (=circumference of tail) is then taken at the mid-point of its length; likewise the width of the tail stripe. The ratio between the two readings is next determined, the width of the dorsal stripe being expressed as a percentage of the circumference of the tail. The following are the figures for the four races and the two sexes, the figure in parenthesis representing the number of animals measured:[7]

TABLE I

| | |
|---|---|
| *rubidus,* ♂ (69) | $42.51 \pm 0.45$ |
| *rubidus,* ♀ (50) | $41.96 \pm 0.53$ |
| Berkeley *gambeli,* ♂ (24) | $36.08 \pm 0.80$ |
| Berkeley *gambeli,* ♀ (28) | $35.50 \pm 0.56$ |
| La Jolla *gambeli,* ♂ (85) | $32.08 \pm 0.33$ |
| La Jolla *gambeli,* ♀ (46) | $32.43 \pm 0.49$ |
| *sonoriensis,* ♂ (74) | $27.49 \pm 0.32$ |
| *sonoriensis,* ♀ (59) | $28.92 \pm 0.36$ |

6a This condition I have recently found to occur in occasional specimens of *rubidus* trapped near Carlotta, California.

7 Since this character was not measured when these studies were first commenced, the number of individuals included in the present table falls far short of those measured for some other characters.

While the statistical certainty of these four types can not be doubted, it must again be insisted that the differences relate to averages rather than to individual animals. The frequency distributions of the various widths, as represented by the histograms (Fig. 5), show this point clearly. There is a certain amount of overlapping, even between the most divergent races.

*Skin Pigmentation.*—Certain regions of the skin are colored by dark pigment. The regions showing skin pigmentation most clearly are the ears, tip of snout, soles of feet, and, in the males, the scrotum.

Frequent comparisons of considerable numbers of freshly killed specimens have made it plain that, in respect to the pigmentation of the ears, our four races can be arranged in the same graded series as was found to hold for coat color. As regards the other three skin characters, I have never compared more than two races at a time, but I feel little doubt that all four could be arranged in the same order. No exact measurements are here possible, as in the case of the tail stripe. In a few instances I have, however, graded a given character, according to an arbitrary scale, and have thus been able to express the differences between two races in a roughly quantitative way. The following comparison between 42 *sonoriensis* and 38 La Jolla *gambeli* with respect to the pigmentation of the scrotum will illustrate this point.

TABLE II

| | *sonoriensis* | | *gambeli* | |
|---|---|---|---|---|
| | Number of Cases | Percentage | Number of Cases | Percentage |
| Heavy | 1 | 2.4 | 3 | 7.9 |
| Moderate | 3 | 7.1 | 2 | 5.3 |
| Slight | 5 | 11.9 | 7 | 18.4 |
| Very slight | 1 | 2.4 | 4 | 10.5 |
| None | 32 | 76.2 | 22 | 57.9 |
| Total | 42 | 100.0 | 38 | 100.0 |

A similar tabulation was made in another case, comparing two lots of specimens of these same races in respect to the pigmentation of the foot.

It might readily be contended that all these various pigmental differences, which have thus far been considered, are merely manifestations of some general tendency toward a given degree of pigmentation of the body as a

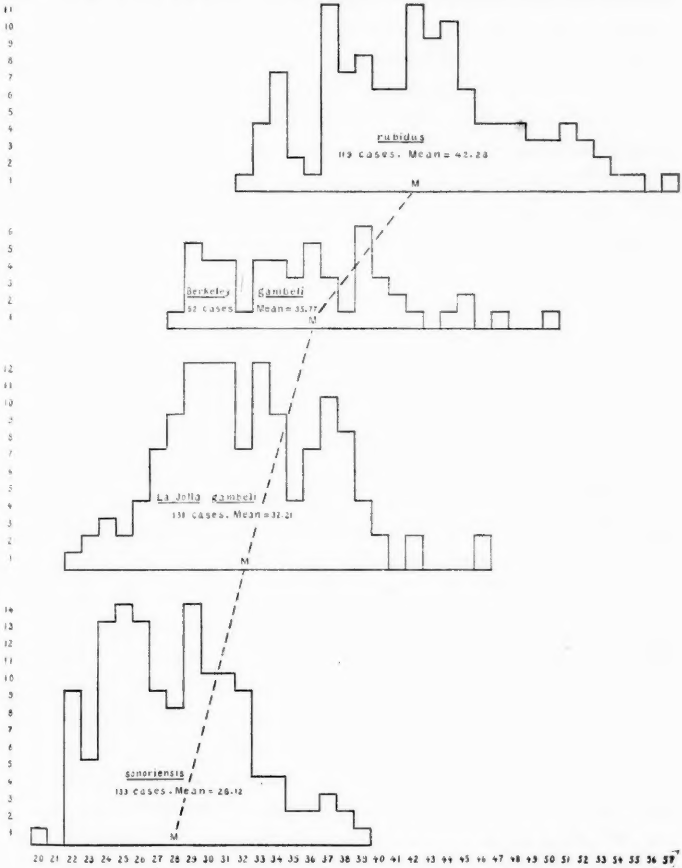


FIG. 5. Histograms, showing the frequency distributions of the percentage values for the width of the tail stripe (ratio to circumference) in the four races here considered (sexes combined).

whole. This tendency perhaps manifests itself in a greater or less intensity or extensity, or both. In the absence of exact quantitative standards, it is impossible

to determine whether or not these various pigment characters are correlated. If they are, the correlation is certainly not a close one, as frequent observations have shown. For example, the grade of foot-pigmentation was determined for the paler and darker halves of a series of *sonoriensis* and also for a series of *gambeli*. In both cases the average grade for the foot was slightly greater for the darker half than for the paler; but the difference was so small that I am not sure of its significance. Again, in the lot of 38 *gambeli* comprised in Table II the darkest individual (dorsally) and the one with the darkest feet were both devoid of visible pigment on the scrotum. Similar entries are frequent among my notes.

### 2. *Structural Differences*

The structural features which I have subjected to quantitative determination are (1) *weight*, (2) *body length*, (3) *tail length*, (4) *foot length*, (5) *ear length*, (6) *number of tail vertebræ;* together with several other skeletal characters which I shall not discuss in the present paper. The methods employed throughout these studies will be described more fully in a later report. A brief statement will suffice for the present. Body length, as here employed, is the total length, minus the length of the tail. In taking the total length, a special contrivance is employed, the body being stretched slightly and to a uniform extent. A constant procedure is likewise employed in measuring the tail length. The figure recorded for the latter represents the distance from the first free caudal vertebra to the tip of the tail, under a uniform degree of tension. The ear length here used is that from the summit of the "notch" to the tip of the ear. Foot length is the distance from the heel to the tip of the claw of the longest toe, the foot being pinned, sole downward, to a blackened board.

The statistical methods employed in analyzing these data have been rather fully discussed in a former paper (1915), to which the reader is referred.

(1) *Weight* and (2) *body length* are not dealt with directly in the present comparisons. The former is an index of metabolic condition as well as of size (*i. e.,* length). Captive mice, for example, are commonly fat in comparison with wild ones. *Body length* is of little significance in comparing two groups of mice, unless we know, either that the animals are all of the same age, or that the limit of growth has been reached by all of them. These things are frequently impossible to determine.

(3) *Tail length* is dealt with, both as an absolute value and as a percentage of the body length. If absolute tail lengths are to be compared in two groups of animals, the comparison can only be made between animals of approximately the same body length. My practise is to divide each series into a number of size-groups, differing by only two millimeters of body length. Group 80–81 of one series is then compared with group 80–81 of the other, group 82–83 with group 82–83, etc. The graphs (Figs. 6 and 7 and 9–12) are based upon this procedure. Each "curve" connects the means of the size-groups of each series of animals, the abscissas representing body length, the ordinates the character under comparison. In order to eliminate very young mice, groups having body lengths of less than 80 mm. are omitted. Even so, it is likely that most of the animals in the lower groups of the series are immature, but this fact in no way affects the validity of the comparisons.

It will be seen, from an inspection of the figures (6 and 7), for both males and females, that, as regards tail length, the Eureka mice (*rubidus*) stand in a class by themselves. In comparison with the wide interval between this long-tailed race and the other three races here considered, the latter differ but slightly among themselves. It is evident, none the less, that the La Jolla animals have somewhat longer tails than do those from Berkeley or Victorville, while the last two agree fairly closely in their mean condition.

Relative tail length, *i. e.,* the length of the tail expressed

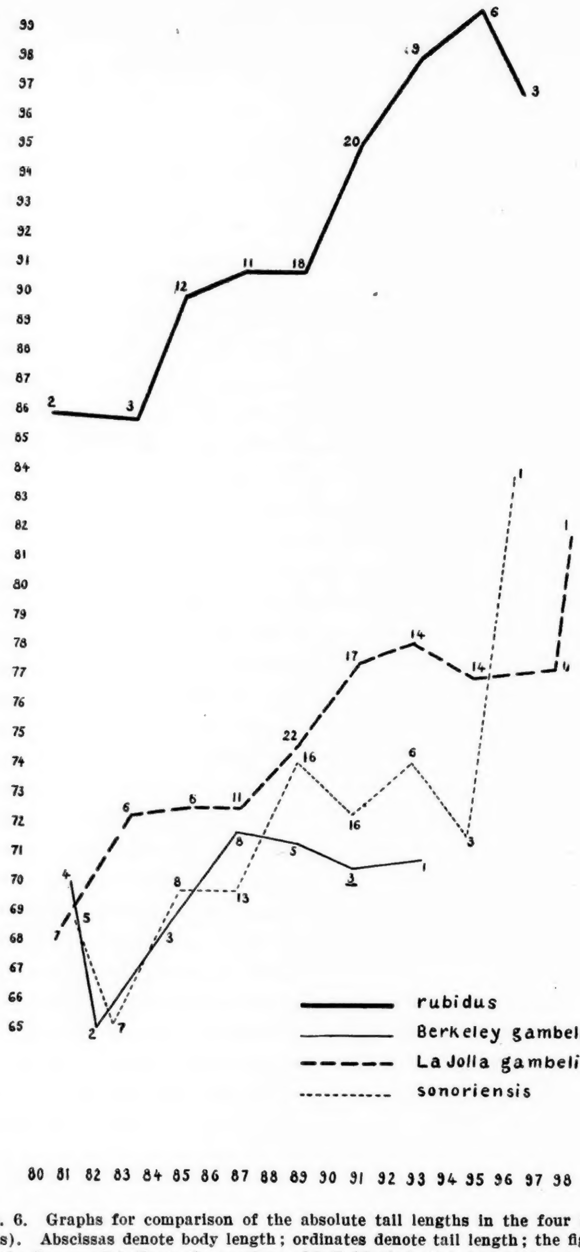


FIG. 6. Graphs for comparison of the absolute tail lengths in the four races (males). Abscissas denote body length; ordinates denote tail length; the figures along the "curves" indicate the numbers of individuals in the various size groups.

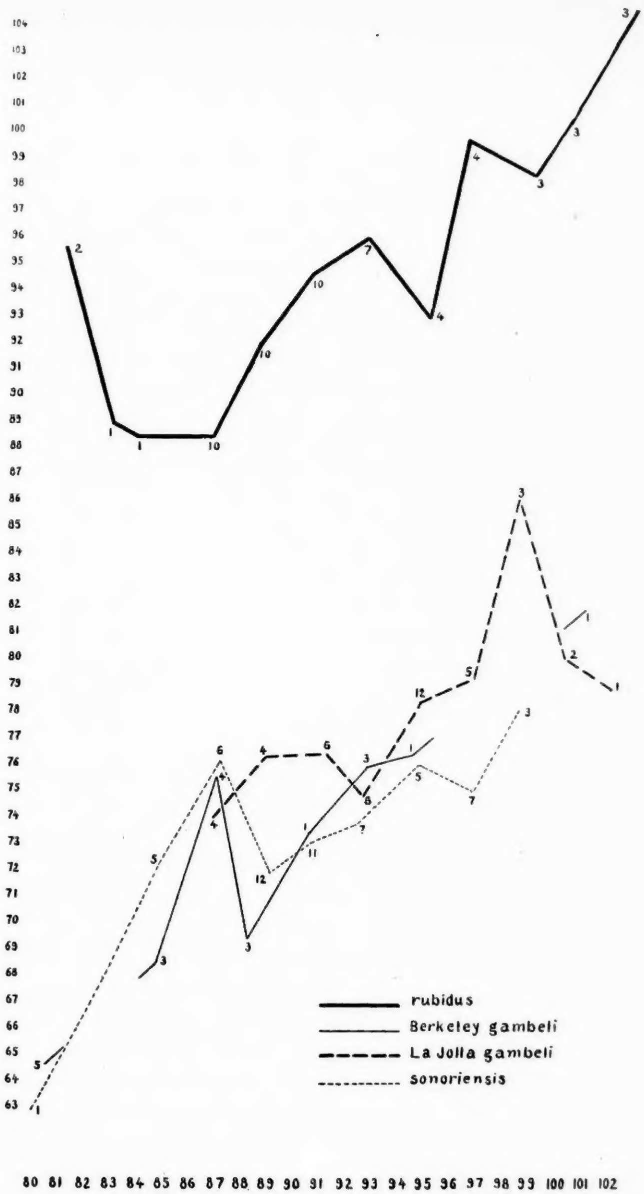


FIG. 7. Comparison of the absolute tail lengths in the four races (females).

as a percentage of that of the body, is to a considerable extent independent of the size of the animal. Larger mice, it is true, have relatively somewhat shorter tails than do smaller ones. But the differences are so slight that they may be overlooked, unless the mean size of the two groups under comparison differs considerably. The relative tail lengths of our four races of mice may be compared in the following table.[8] This shows the same relations as were portrayed by the graphs. It also shows that there are no significant differences between the sexes as regards the length of this member.

TABLE III

| | |
|---|---|
| *rubidus*, ♂ (84) | 104.45 ± 0.38 |
| *rubidus*, ♀ (57) | 103.37 ± 0.52 |
| Berkeley *gambeli*, ♂ (26) | 81.69 ± 0.55 |
| Berkeley *gambeli*, ♀ (21) | 81.76 ± 0.65 |
| La Jolla *gambeli*, ♂ (99) | 84.36 ± 0.35 |
| La Jolla *gambeli*, ♀ (45) | 83.04 ± 0.43 |
| *sonoriensis*, ♂ (75) | 81.29 ± 0.44 |
| *sonoriensis*, ♀ (61) | 81.30 ± 0.45 |

The distribution frequencies for these various lengths are represented by the histograms (Fig. 8). From these it is evident that only an occasional Eureka mouse has as short a tail as the longest tailed members of any of the other three races. The latter, however, differ from one another but slightly.

(4) In respect to *foot length* likewise (Figs. 9, 10) the Eureka mouse is very distinct from the other three races, while the latter show no significant differences among themselves. It is of interest, however, that in all four of these races the female has, on the average, a slightly shorter foot than the male. If any one still entertains the

[8] Owing to a slight change in the manner of measurement, which was made after these studies were commenced, the tail lengths of the earlier animals of my series have been rejected from the computations. This procedure has affected particularly the numbers of the Berkeley series.

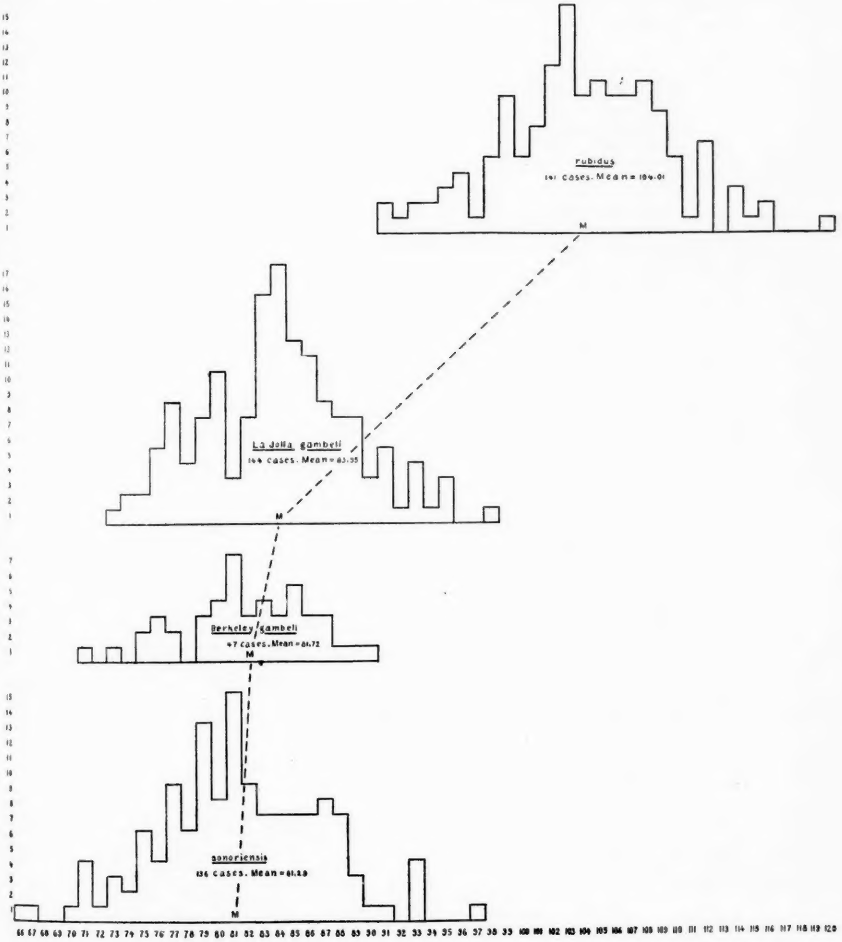


FIG. 8. Histograms, showing the frequency distributions of the percentage values for the length of the tail (ratio to body length), in the four races (sexes combined).

notion that small feet, along with other feminine charms in mankind, are due to "sexual selection," the situation in *Peromyscus* ought to give him pause.[9] The mean dif-

[9] This same difference was found by me to hold for white mice, at least for full grown individuals (1915, pp. 358, 367).

ferences between males and females, computed according to a method earlier described by me (1915, pp. 345, 346), are:

| | |
|---|---|
| *rubidus* | 0.31 mm. ± .08 |
| *gambeli* (Berkeley) | 0.29 mm. ± .05 |
| *gambeli* (La Jolla) | 0.09 mm. ± .07 |
| *sonoriensis* | 0.38 mm. ± .05 |

(5) In respect to *ear length*, we find a quite different set of relations. It is the La Jolla mouse in which these appendages are the longest, the Berkeley mouse in which they are the shortest, while the redwood and the desert animals occupy an approximately intermediate position and scarcely differ significantly from one another. It is here to be noted that the two extremes of the series, in respect to this character, have been placed by the systematists in the same "subspecies" (*gambeli*).

(6) The counting of the *tail vertebræ*, like the other measurements of skeletal characters, has not yet been completed. I have, however, determined the number in 25 specimens each of the Eureka, La Jolla and Victorville races. The fifth vertebra, counting from the most anterior one in the sacrum, has been regarded as the first of the caudal series. The averages and the frequency distributions are indicated in the following table.

TABLE IV

| | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | Average |
|---|---|---|---|---|---|---|---|---|---|---|
| *rubidus* | | | | 2 | 9 | 6 | 5 | 1 | 2 | 28.0 |
| *gambeli* (La Jolla) | | | 4 | 5 | 13 | 3 | | | | 26.6 |
| *sonoriensis* | 1 | 2 | 8 | 7 | 6 | 1 | | | | 25.7 |

The significance of these differences seems highly probable, despite the small numbers. That between *rubidus* and *sonoriensis* can hardly be questioned. It seems plain, however, that the differences in tail length between these various races is not accounted for by the differences in the number of the vertebræ. Thus the Eureka mouse has a mean tail length which is 28 per cent. (of the smaller number) longer than that of the desert mouse. The pre-

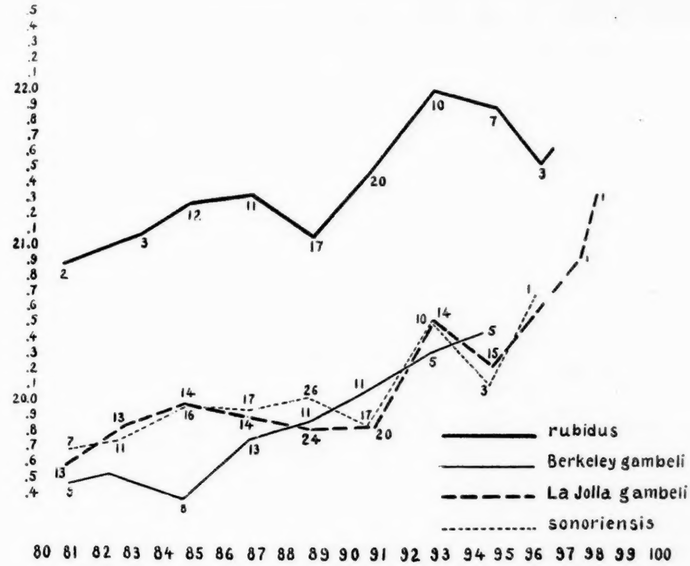


FIG. 9. Comparison of foot-lengths in the four races (males).

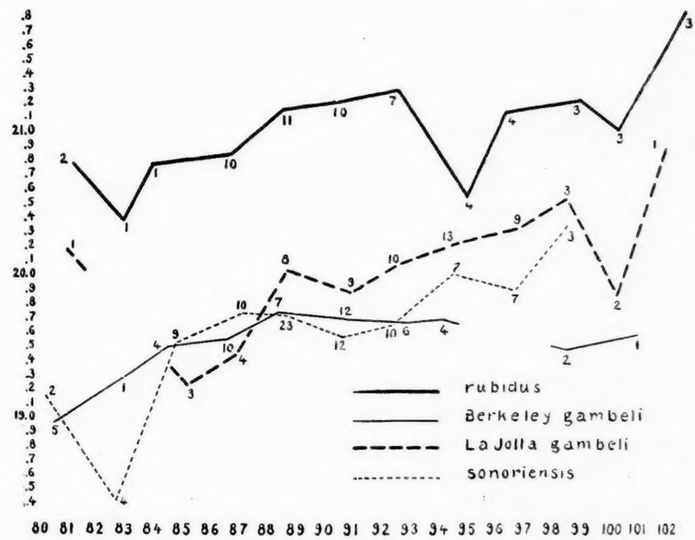


FIG. 10. Comparison of foot-lengths in the four races (females).

ponderance in the number of vertebræ is only 9 per cent. The differences in the length of this appendage are therefore due partly to the number of vertebræ, but chiefly to the length of the individual vertebræ.

*Résumé of Racial Differences.*—In relation to the vari-

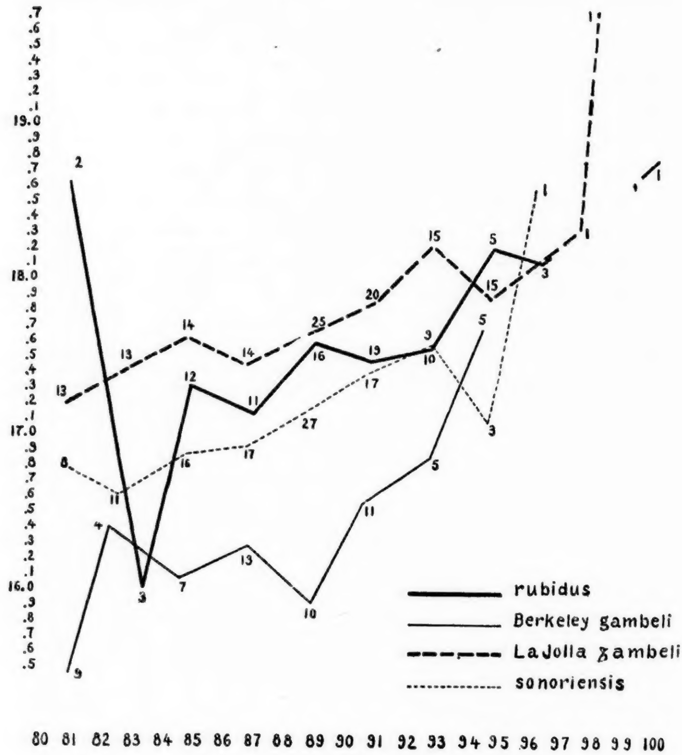


FIG. 11. Comparison of ear-lengths in the four races (males).

ous pigmental differences, those both of intensity and extensity, the four races under consideration were found to present the following graduated series:

Eureka > Berkeley > La Jolla > Victorville.

As regards the length to the tail, the series became:

$$\text{Eureka} > \text{La Jolla} > \begin{cases} \text{Berkeley,} \\ \text{Victorville.} \end{cases}$$

When the number of caudal vertebræ was considered, we had the same arrangement as the last for the three races for which determinations had been made, viz.:

Eureka > La Jolla > Victorville.

In respect to foot length, the following order held:

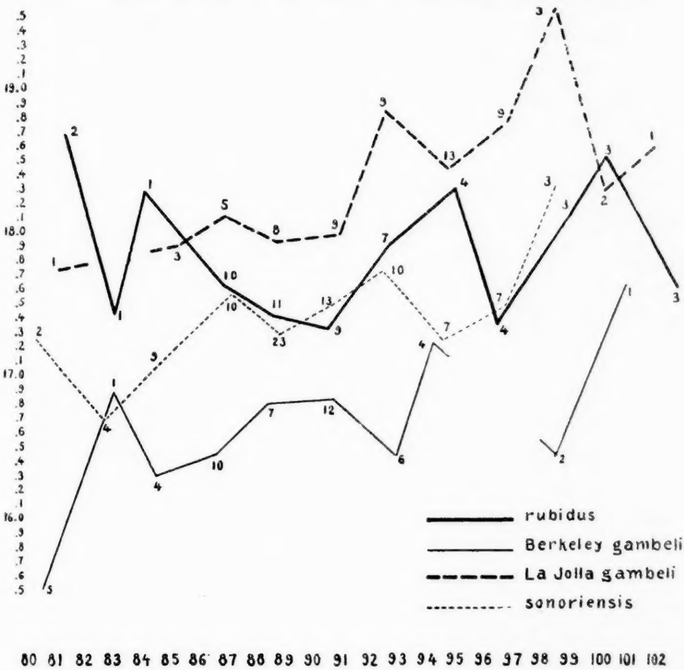


FIG. 12. Comparison of ear-lengths in the four races (females).

$$\text{Eureka} > \begin{cases} \text{La Jolla,} \\ \text{Berkeley,} \\ \text{Victorville.} \end{cases}$$

Finally, as regards ear length, we had a quite different alignment, viz.:

$$\text{La Jolla} > \left\{ \begin{array}{l} \text{Eureka} \\ \text{Victorville} \end{array} \right\} > \text{Berkeley.}$$

It is plain that these "subspecies" have diverged from one another in respect to characters which have varied

quite independently. There is no single graded series for all the characters, which would lead us to suppose that they are in some way correlated or "linked" together.

When pigment characters alone are considered, the Berkeley mice are certainly intermediate between the La Jolla and the Eureka ones, and to that extent may be said to "approach *rubidus*."[10] But this is not true of the length of the tail, the foot or the ear. Indeed, as regards the first of these appendages, the Berkeley race diverges even farther from the Eureka race than does that of La Jolla.[11]

The question whether any of these various character differences may be physiologically or genetically linked together, so as to exhibit concomitant variations, is an interesting one, which I hope, in time, to treat rather fully. But I have already computed coefficients of correlation between two pairs of characters, viz.: between tail length and width of tail stripe, and between tail length and foot length.

In obtaining the former, I have based the coefficients upon the deviations from the mean *relative* tail length of each race and each sex, taken separately. Of these coefficients, three are positive and five negative. They range from $-0.23$ to $+0.09$, the mean being $-0.03$. Thus, it is plain that there is no appreciable correlation, within a single race, between the width of the tail stripe and the length of the tail, despite the fact that these characters seem to be associated, when certain darker races of the northwest coast are compared with more southward ranging forms.

There is, however, a quite marked correlation between the length of the tail and that of the foot. I do not here refer to the obvious fact that larger animals have larger

[10] Osgood, 1909, p. 69. This author likewise states that Berkeley specimens are "longer-tailed than typical *gambeli*."

[11] This conclusion is strengthened by consideration of an even larger series of Berkeley mice which were not included in Table III. The two sets were trapped in two different localities in the Berkeley hills.

tails and likewise larger feet than smaller animals. My figures show that, *even when animals of the same body length are considered,* those with longer tails tend, on the whole, to have longer feet, and vice versa. To obtain these results, I have computed the coefficients separately for each size-group, containing ten or more individuals.[12] All but 5 of these 21 figures are positive, the mean being +0.27. Thus the greater tail and foot length of the Eureka race may have arisen simultaneously, both being the expression of a single constitutional change.

One further word regarding the nature of these racial differences, before we pass to a consideration of their heredity. It is plain that, with a single possible exception, all of the differences thus far considered are "substantive," rather than "meristic," to follow Bateson's[13] terminology, or "proportional," rather than "numerical," to use terms recently employed by Osborn.[14] In no case are they of the nature of "presence-and-absence" differences, such as figure so widely in Mendelian literature. Whether or not, on ultimate analysis, they can be resolved into the latter category, will be discussed later.

The differences without exception relate to means and modes, as was illustrated above by histograms constructed for two of the characters (Figs. 5 and 8). The frequency polygons commonly overlap broadly, when adjacent members of the series are compared. We find an approach to discontinuity only in a comparison of the most widely divergent races.

The single difference of a meristic or numerical character is that relating to the number of caudal vertebræ. But even here the difference is one of averages, for no single race seems to be characterized by the unvarying presence of any particular number of vertebræ, as certain larger taxonomic groups are characterized by a definite number of teeth or mammæ. It is worth mention also that

[12] Cf. Sumner, 1915, pp. 349–350, 409–415.

[13] 1894, pp. 22, 23.

[14] 1915, p. 199. In the paper referred to, Osborn has given some attention to the case of *Peromyscus.*

the last one or two caudal vertebræ are commonly rudimentary, so much so that it is not always easy to determine their exact number. It is scarcely more fitting to apply the term "meristic variation" here than it would be to apply this term to such variations in the number of cells as distinguish a larger from a smaller foot or ear.

(*To be concluded.*)

# INTERNAL FACTORS INFLUENCING EGG PRODUCTION IN THE RHODE ISLAND RED BREED OF DOMESTIC FOWL II

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*Cycles.*—By cycles of egg production are understood the existence of periods of egg production alternating with periods either of decreased egg production or entire cessation of egg production. These cycles may be either long or short. The long-term cycles may have a period of a year. Shorter cycles exist with a period of three or four months, *i. e.,* winter, spring and summer and fall. There are still shorter cycles with periods measured in weeks, while one may also recognize irregular cycles. A litter, as defined by Miss Curtis ('14), is a short period of egg production alternating with a non-productive period and is well illustrated by broody birds, though it may occur in non-broody individuals. A "clutch," according to Miss Curtis, is the set of eggs produced on consecutive days. Its termination is marked by the appearance of a blank day.

The form of the yearly cycle depends to a considerable degree upon some of the internal factors under discussion, that is, it varies in different individuals. Egg production, as a rule, begins in the fall and winter, and continues at a fairly constant rate in most individuals until spring, when the rate rises somewhat in many individuals. Those that have been laying at a relatively high rate do not show this acceleration, at least not in as marked a degree. Sooner or later in a broody race broody periods appear, which interrupt egg production at fairly constant intervals. The rate, however, during the nonbroody periods shows no slackening, but on the contrary a very slight acceleration may be demonstrated, so

that the lower egg production noted after the first broody period is due solely to the interruption of production. During the summer, the rate of egg production slackens, due almost entirely to the broody periods. The data for the 1913–14 flocks show that after June the rate of production is about constant for the next three months, largely because the first of July marks the point at which practically every individual in the flock has entered on its broody portion of the year. Some time in the late summer or during the fall, the various individuals stop laying and moult, some at one time, some at another, but usually at the end of a broody period. After the rest period in the fall, the birds gradually begin to lay again in mid-winter, somewhat as they did as pullets, except that the rate is slower as a rule. Except for this feature, the character of the second year's production is much the same as the first.

The winter cycle is regarded by the workers at the Maine Station (Pearl, '12) as the most important of all the cycles, at least from the standpoint of the investigation of the inheritance of egg production. They have found that it represents a definite period in the life history of the individual, among their Barred Plymouth Rocks. Furthermore, during this period, the greatest differences are to be observed in the egg production among individuals. They also find that high winter egg production is correlated with annual egg production, as would be expected except in the event that high egg production early in life tends to lower production in later life. In other words, a bird that is a good layer during the winter is probably a good layer at all times. There are other reasons, mostly of a practical nature for the use of the winter cycle as a measure of fecundity.

Taking the year as a basis the workers at the Maine Station recognize as its first characteristic the winter cycle beginning with the first egg of the pullet and extending to March 1. This date is taken as a convenient working point that falls near the biological division point.

During this period, flock production rises from zero to a maximum and then slows down somewhat toward its close. This slackening is due to a cessation of production on the part of most individuals while nearly all show at least a slackening of egg production towards the close of the winter cycle. The exact date at which the cycle ends varies with the individual, and may occur at almost any point during the winter months including March. Miss Curtis ('14), in another connection, has published the monthly records of a few hens that show this cycle. They are shown in Table VII. With one exception, No. 236, the birds all laid over 30 eggs. The evidence for a winter cycle is shown by the depressed egg production in January and February and is very clear. The records published by Gowell, '02, '03, also show this point.

TABLE VII

A PORTION OF TABLE XXV FROM CURTIS ('14) SHOWING THE WINTER EGG PRODUCTION OF A NUMBER OF BARRED PLYMOUTH ROCK PULLETS. THE DECREASED PRODUCTION IN JANUARY AND FEBRUARY OVER THE DECEMBER RECORDS IN NINE INSTANCES IS EVIDENCE OF A WINTER CYCLE.

| Month | Pullet Number | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 218 | 139 | 446 | 516 | 192 | 259 | 204 | 478 | 212 | 184 | 211 | 236 | 441 |
| 1910 | | | | | | | | | | | | | |
| October | ... | 3 | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... |
| November | 15 | 19 | 17 | 15 | 18 | 8 | 5 | 13 | 6 | 12 | 8 | 1 | 9 |
| December | 25 | 18 | 27 | 24 | 24 | 11 | 16 | 24 | 8 | 14 | 15 | 0 | 18 |
| 1911 | | | | | | | | | | | | | |
| January | 13 | 19 | 6 | 9 | 14 | 13 | 4 | 10 | 11 | 6 | 5 | 0 | 14 |
| February | 13 | 10 | 15 | 9 | 0 | 16 | 13 | 0 | 8 | 11 | 5 | 0 | 16 |
| Winter total | 66 | 69 | 65 | 57 | 56 | 48 | 38 | 47 | 33 | 43 | 33 | 1 | 57 |

Pearl and Surface, '11, describe the other periods as follows:

> The next period (March, April and May) is the natural laying season. It corresponds to the egg-laying part of the natural reproductive cycle exhibited by the wild *Gallus*. . . . Naturally, therefore, a high mean and a low variability in production are exactly what we find characterizing the laying in each of the months of this period.
>
> The third period (June, July and August) is characterized by a gradually falling mean production and a variability gradually increas-

ing. . . . This is the period in which the rearing of the chickens naturally occurs and it also represents an extension of the breeding season.

The fourth period (September and October) is not easily separated from the third in respect to laying, but in general it is the period of moulting. . . . It is characterized by reduced laying and marked increased variability.

It is not clear from their accounts whether or not they consider that these periods extend through the second year or whether they are to be considered as characteristic solely of the pullet year.

Just how far the data on Barred Plymouth Rocks are applicable to our Rhode Island Reds is somewhat uncertain. At the outset it is evident that the small percentage of birds that show an interruption in their winter laying because of the presence of a broody period afford no evidence either for or against the existence of a winter cycle. Of the birds that do not go broody during the winter two classes can be distinguished, viz., those that show an interruption in their winter laying and those that do not. In the 1913–14 flock and in the 1915–16 flock from the original source, a large percentage of the birds show no interruption in production, not even a slump in the rate of production. Such birds lay at an approximately constant rate through the late fall and winter months, and on through the spring. Among the records of the main portion of the 1915–16 flock are many that show an interruption or else a slackening of production. Of these birds it can be said that they have a winter cycle. But there are two points about these records that make it difficult to interpret the interruption in production as an index of a cycle. First, the interruption may occur at almost any time during the winter followed by a resumption of production in mid-winter, and second, some individuals show more than one period of nonproduction. While there is definite evidence that a winter cycle exists in *some but not all* Rhode Island Reds, the possibility that some at least of these interruptions of production may be due to environmental factors must be fully recognized.

As already noted, there are many Rhode Island Reds which show no sign of a winter cycle. Whether this means that such birds do not have a winter cycle, or whether it means that some other factor covers up an underlying cycle is uncertain. In many instances these birds are very much like the Barred Plymouth Rocks noted by Pearl and Surface, '11, who state:

> Many birds of course have no proper winter cycle at all. They begin to lay for the first time in January or February and keep on laying without any large break straight through the spring cycle.

But there are many other Rhode Island Reds that begin to lay in October, November and December and lay through the winter and spring without any breaks whatsoever. Moreover, those birds that begin to lay in January or February for the first time very rarely show any break whatsoever. For these instances where the birds begin to lay late in the winter it is conceivable that the winter cycle might extend well into March but that the comparatively mild weather at that season of the year would tend to eliminate the rest period and thus conceal the winter cycle. But this argument cannot be applied to those instances in which the laying is continuous from its start in October, November or December right through the spring. There seems no reason to speak of a winter cycle for this class of Rhode Island Reds.[4]

The spring cycle, in Rhode Island Reds, in so far as it can be differentiated from the winter period, differs chiefly from that of the Barred Rocks in extending nearly through June, since the end of June marks the point at which practically every bird that will go broody has become broody at least once. Egg production is at its maximum at the beginning of this period due to active laying on the part of practically all individuals but falls sharply

[4] Later work on this point demonstrates, beyond doubt, that the presence of a definite winter cycle is not characteristic of our strain of Rhode Island Reds as a whole. There is some evidence, moreover, that the winter cycle is a Mendelian recessive, the dominant allelomorph being continuous winter production. For details see Goodale, '18.

after its middle, the rate of decline being much greater than for the Barred Plymouth Rocks.

The summer period may be considered to be July, August and September. Practically all the birds of the flock are laying in broody cycles with egg production remaining at approximately a constant level, while considerable partial moulting is going on. It passes gradually into the fall period which is characterized chiefly by the cessation of egg production—usually coinciding with a broody period—and the onset of the fall moult together with some slowing in rate of production of those birds that are laying. Biologically the fall period overlaps the calendar year since it may extend into December. The question of egg production in the fall, at the end of the pullet year, is on rather a different basis from that of the other seasons of the year. The egg producing mechanism of the hen seems to be in a peculiarly unstable condition and unless great care is exercised may cease functioning in response to slight adversities in environment. Some hens, however, and this is really the important point, continue to lay throughout the fall months with the same regularity they exhibited in the spring. This affords us an opportunity to build up a strain of birds that will be persistent layers throughout the year.

Thus, persistency in egg production through the fall months enters in as a factor in determining the total egg production as has also been emphasized by Rice ('14). Some birds cease laying relatively early in the fall, say late in August or September; others, however, of the same age, breeding, and under the same conditions, continue to lay all through the fall, at approximately the same rate of production as during the summer months, although the rate may fall off slightly. Now, these birds will have quite a different total record from those that stop early in the season and if one examines his records he finds that while many persistent layers are also good producers early in the season, nevertheless a great many of the birds that were good layers during the winter are

not persistent layers during the fall, while some birds with low winter records are good fall layers.

Other kinds of cycles, which are described in the following paragraphs, have been noted in the Rhode Island Reds. In broody individuals, where the practice is followed of "breaking up" the hen, a series of cycles is introduced, marked by broody periods alternating with an egg production period. If the natural course of events is not interfered with in the case of broody hens, the broody period lasts until the chicks have hatched. Then the period of rearing takes place. Toward the end of this period the hen begins to lay and the cycle is repeated.

There is also a short time cycle of one or two weeks which needs little discussion at present. It is shown by an acceleration in rate of egg production followed by a decline somewhat as follows: Egg—blank—egg—egg—blank—egg—egg—egg—blank—egg—egg—egg—egg—blank—egg—egg—egg—egg—blank—egg—egg—egg—blank—egg—egg—blank—egg—blank—egg—blank—egg—blank—and repeat. Although one often finds records that approximate closely the above scheme, their rarity suggests either that the fluctuations in rate are due directly to some extraneous circumstance or, if there is a fundamental rhythm of this sort, that it is subject to disturbance from the environment. Whatever may be the cause, at present it is doubtful if it is indicative of an internal factor.

The next type of cycle is that exhibited by certain hens which lay at a relatively high rate for a time and then stop. This period may correspond to the term often used by poultrymen when speaking of a hen's clutch. Here again we are confronted by doubt as to the causation of these blanks, for many hens do not have such pauses in production. Once they begin laying they continue without any considerable vacant period (not exceeding three or four days) until the onset of the first broody period.

*Stamina.*—A strong bird is readily distinguished from a weak one, but it is difficult to separate the birds per-

manently according to a definite standard since it is impossible to secure a constant environment. A fairly uniform environment in the sense that all birds are exposed to the same external conditions at any one moment is fairly easily secured; but since the external conditions, particularly weather conditions, are very variable and follow no definite course, and since a bird's vigor is a resultant of its own inherent strength of resistance against the environment, it is clear that the objective vitality observed in each member of a flock may be unequally affected by the surroundings.

The evidence available on the relation of vitality to fecundity thus far points in two more or less opposite directions. Many birds of low vitality have made not only excellent but even high records. On the other hand, birds of strong vitality may make low records. At the same time there is a point at which the vitality becomes too low for good egg production. In the fall of 1913, thirty-eight birds graded early in the fall, before laying commenced, as "poor" in respect to vigor, were put in the laying houses. They had an average record for the winter period of only 20 eggs against an average of 38 for the entire flock, including the poor birds. Low vitality evidently depressed egg production in this instance; mainly, through retardation of the time of commencement of laying rather than by slow production. The influence of lack of vigor on winter egg production is shown in Fig. 9, where the curve of winter egg production for the entire flock is represented by the continuous line and that for the "poor" birds by the dotted line.

Occasionally, birds of low vitality may make excellent egg records. In one family in particular, the birds were of distinctly mediocre quality, as evidenced by their weight, activity, hatching quality of eggs and viability of chicks and yet they were able to make high records, the average for the family of seven individuals being 63.3—ranging from 33 to 81—for the winter period, with a yearly average of 192.4 for the five birds that survived throughout the year, and with a range of 154 to 210.

*Moult.*—Moulting exercises some influence on the number of eggs produced, since birds that are moulting often do not lay, particularly during the fall moult. Moulting itself may be induced at certain seasons of the year by changes in management, especially those changes that tend to stop egg production. Such changes apparently change the course of the metabolism of the bird. Broodiness in late summer and early fall appears to be a common cause of the onset of a moult and consequent cessa-

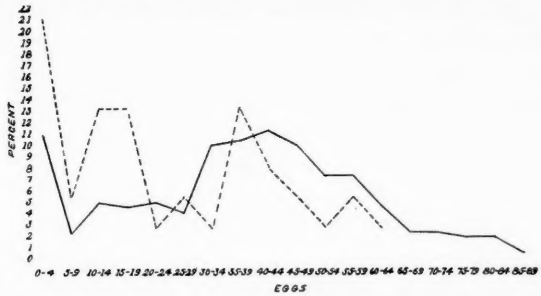


FIG. 9. The effect of low vitality on winter egg production. The graph shows the percentage of the flock of 1915–16 laying the specified number of eggs. The continuous line is for the entire flock. The dotted line is for that portion of the flock graded "poor" or of low vitality, before being placed in the laying houses.

tion of egg production. At least one might draw this conclusion from the fact that egg production, as the usual rule, ceases with a broody period, for in most instances the last egg laid in late summer or early fall coincides with the beginning of a broody period. It is not clear, however, whether the moult starts because the bird has reached the limit of her production period, or whether the moult begins because of the interruption to egg production due to the onset of the broody period.

In the Rhode Island Reds we have observed a partial moult that begins in the early part of the summer and as a rule seems to affect egg production very little. In the autumn this partial moult is followed by a more extensive (often complete) moult attended by cessation of production. It is possible that the summer moult has been in-

duced by broodiness, but that the hens are broken up so quickly and the impulse toward resumption of egg production at this season is so strong that it inhibits the moult at various stages.

Pullets that begin to lay very early in the fall very often undergo a moult during the latter part of the same fall. It is not clear that early production of itself tends to induce the moult so long as the birds affected are not hatched too early in the season. The moult is more commonly observed in pullets that are hatched very early in the season and which begin to lay in August and September. Such birds rarely make a continuous record but instead stop laying after producing a variable number of eggs and moult much like birds from fifteen to eighteen months of age. In the flocks with which we have been dealing the variability in maturity has induced some complications in handling the flocks. If an attempt is made to hatch birds sufficiently early in the season, so that a good share of them will begin laying in November, some begin too early, lay a while, and then moult.

*Rate and Rhythm of Production.*—The percentage rate of production at any time and for any period may be taken as the number of eggs times 100, divided by the length of the period involved, measured in days. Rate is an important factor in determining egg production, but in the Rhode Island Reds is of quite secondary importance as compared to date of first egg (and of course age at first egg).

The distribution of the percentage rate calculated for the winter period (between the first egg of each pullet and March 1) for the flock of 1913–14 has been determined and the graph shown in Fig. 10 plotted. The curve shows a considerable homogeneity of rate in the flock. Since the general trend of events, such as accidents, temporary ailments, etc., is of such a nature that some birds do not attain their natural inherent rate, the curve shows a very gradual slope at the left-hand side up to about 30 per cent., a somewhat more rapid rise be-

tween 30 and 50 per cent. and a much sharper rise beyond 50 per cent. The mode comes at the 61 to 70 per cent. group, while the maximum rate does not exceed 90 per cent. It is interesting to note that 8.5 per cent. of the

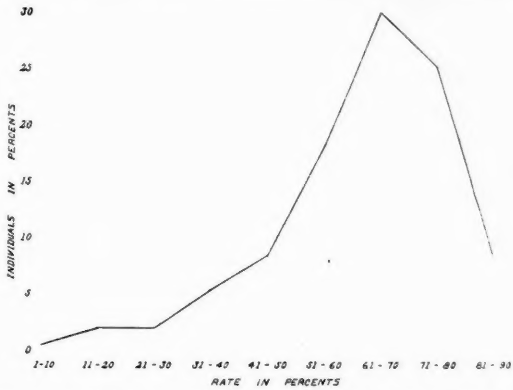


FIG. 10. Percentage rate of production for the winter period. The percentage of the flock laying at the specified rate is shown by the ordinates, the rate by the abscissæ. Flock of 1913–14. M = 62.50, S. D. = 15.77, C. V. = 25.23.

flock laid at a rate exceeding 80 per cent. for the entire winter period.

The effect of variability in rate on total production for a definite period is shown by the records given in Fig. 11.

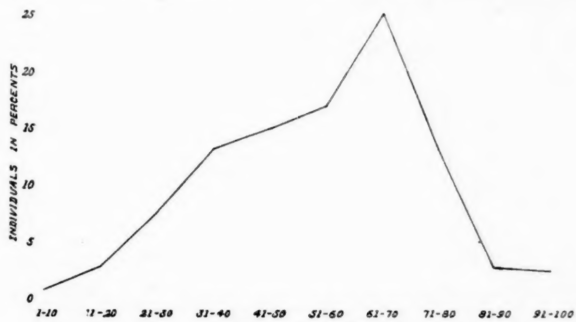


FIG. 10*a*. Percentage rate of production for the winter period. The percentage of the flock laying at the specified rate is shown by the ordinates, the rate by the abscissæ. Flock of 1915–16. M = 54.59, S. D. = 18.52, C. V. = 33.93.

No. 49 HATCHED MARCH 16, 1913. AGE AT FIRST EGG, 248 DAYS

| Date 1913–14 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | Totals | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Nov. | | | | | | | | | | | | | | | | | | | / | / | / | | / | / | / | / | / | | / | / | ■ | 10 | |
| Dec. | / | / | | / | / | / | / | | / | / | / | / | / | / | / | | / | / | / | / | / | / | / | / | / | / | / | / | / | / | / | 28 | |
| Jan. | / | / | / | | / | | N | / | | / | / | / | / | / | / | | / | / | / | / | / | / | / | / | / | / | | / | / | / | / | 25 | |
| Feb. | / | / | N | / | / | / | / | / | | / | / | / | / | / | / | / | / | / | / | / | / | / | / | / | | / | / | / | ■ | ■ | ■ | 25 | 88 |
| Mar. | / | / | / | / | / | | / | | / | / | / | / | / | / | / | / | | / | / | / | / | / | / | / | / | / | / | / | / | / | / | 28 | |
| Apr. | / | | B L | | | A | N | N | N | N N | N N | N BL | | A N | / | / | / | N | / | / | / | | / | / | / | / | / | / | / | | ■ | 14 | |

No. 4797 HATCHED MARCH 21, 1915. AGE AT FIRST EGG, 236 DAYS

| Date 1915–16 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | Totals | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Nov. | | | | | | | | | | | | / | | / | | / | / | | / | / | | / | / | | / | / | | / | / | | ■ | 12 | |
| Dec. | / | | / | / | | / | / | | / | | / | / | | / | | / | / | | / | | / | | / | | / | / | | / | / | | / | 19 | |
| Jan. | / | | / | | / | | / | | / | | / | | / | | / | | / | | / | | / | | / | | | / | | / | | / | | 15 | |
| Feb. | / | | / | | / | | / | | / | | / | / | / | / | | / | / | | / | | / | | / | / | | / | / | | / | ■ | ■ | 18 | 64 |
| Mar. | / | | / | / | | / | / | | / | / | | / | / | / | | / | / | / | | / | / | / | | / | / | / | / | | / | / | / | 23 | |
| Apr. | / | | / | / | / | | / | / | | / | / | / | | / | / | / | / | | / | / | / | / | | / | / | / | / | / | | / | ■ | 23 | |

FIG. 11. Types of daily egg records with special reference to the winter egg production, although the records for March and April are also shown. All three pullets matured near the average age. No. 49 is that of a pullet that laid continuously at a high rate. No. 4797 is that of a pullet that laid continuously at a rather slow rate of production, while No. 5080 is a pullet that laid intermittently and at a slow rate. This last would seem to be a mediocre producer in Pearl's sense.

Number 49 laid at an exceptionally high rate. On the other hand No. 4797 laid at a rather low rate for a bird that produced eggs continually throughout the winter. Although she began laying several days earlier in the year than No. 49, she produced 24 eggs less, due to her slow but steady rate of production. An entirely different type of rate is shown by No. 5080. This bird is a true mediocre producer in so far as may be judged from her record. She laid her first egg at a fairly early date and fairly early in the season but her rate of production was very low. The eggs, too, were produced at haphazard intervals. Her record is to be compared with that of No. 4568 (Fig. 4), which laid the same number of eggs but all in the last part of February. Records similar to those of No. 5080 are shown by Nos. 274 and 280 (Fig. 12), both Barred Plymouth Rocks in one of the contest pens at the Essex County Agricultural School. Another type of rate is shown by No. 4815 (also Fig. 12), which exhibits also a well-defined winter cycle. This bird matured early, began laying early in the season, and laid well for about six weeks. Then she stopped entirely and did not lay at all again until late in February.

While rate may be considered independently of the rhythm, *i. e.,* rhythm may be ignored; rhythm can not be considered apart from rate. A hen may lay twelve eggs in a month and the rate be described as such or as 40 per cent. without paying any attention to the sequence in which the eggs appear, but if the rhythm be considered, attention must be paid to the sequence between eggs. Thus, two blank days may repeatedly alternate with one blank day between eggs, producing a regular rhythm, or the twelve eggs may be laid in groups of two, three, or more eggs on successive days and then a considerable period of blank days intervene, the rhythm in this instance being irregular. A certain degree of regularity of rhythm is closely associated with high rate of production, though some birds of relatively low rate lay in a regular rhythm (Fig. 11). Most low-record birds, how-

No. 5080 HATCHED MARCH 28, 1915. AGE AT FIRST EGG, 244 DAYS

| Date 1915–16 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | Totals | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Nov. . . . . . | | | | | | | | | | | | | | | | | | | | | | | | | | N | / | | | | ■ | 1 | |
| Dec. . . . . . . | | | | | | | | | | | | | | | | | | | | / | | | | | / | | / | | / | | | 4 | |
| Jan. . . . . . . | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0 | |
| Feb. . . . . . | | | | | | | | | | | | N | NN | | / | | / | | / | | / | | / | / | | / | | | | ■ | ■ | 7 | 12 |
| Mar. . . . . . | / | | / | | / | | / | | | | | | / | | / | | / | | / | | / | / | | / | | / | | / | | / | | 14 | |
| Apr. . . . . . | / | / | | / | / | | / | | / | / | | / | / | | / | / | | / | / | | / | / | | / | / | . | / | / | / | | ■ | 20 | |

FIG. 11. (*Concluded.*)

No. 274 HATCHED 1915. AGE AT FIRST EGG, UNKNOWN

| Date 1915–16 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | Totals | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Nov. . . . . . | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | ■ | 0 | |
| Dec. . . . . . | | | / | | / | | | | / | | | | | | | | | | | | | | | | | / | | / | | | | 5 | |
| Jan. . . . . . . | | | | | | | | | | | | | | | / | | | | | | | | | / | | | / | | | | | 3 | |
| Feb. . . . . . . | | | / | | | | / | | | | | | | | | | | | | | | | | | | | / | / | / | ■ | ■ | 5 | 13 |
| Mar. . . . . . | / | | | | | | | | | | | | | | | | | | | | | | | | / | | / | / | | | | 4 | |
| Apr. . . . . . . | | / | / | | | | | / | / | / | / | | | / | / | | / | / | / | | / | / | / | | | / | | | / | / | ■ | 17 | |

FIG. 12. Daily records of two Barred Plymouth Rocks (Nos. 274 and 284) in the contest conducted by the Essex County (Mass.) Agricultural School. They are mediocre producers. The third record, *i. e.*, of 4815, a Rhode Island Red, shows a long winter rest period, *i. e.*, a winter cycle.

No. 284 HATCHED 1915. AGE AT FIRST EGG, UNKNOWN

| Date 1915–16 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | Totals | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Nov....... | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | ■ | 0 | |
| Dec....... | | | | | | | | | | | | | | / | | / | | | / | | | | | | | | | | | | | 3 | |
| Jan....... | | | | | | | | | | | | | | | | / | | / | / | / | / | / | / | | / | / | / | / | / | / | / | 14 | |
| Feb....... | | | / | | | | / | / | | | | | | | | | | | | | | | | | / | | | | | ■ | ■ | 4 | 21 |
| .......... | | | | | | | / | | / | / | / | | / | / | / | / | | / | / | | / | / | | / | / | | / | | | | | 15 | |
| Apr....... | | | | / | | / | | | | / | | / | / | / | / | | / | | | | | | | | | | / | | / | / | ■ | 11 | |

No. 4815 HATCHED MARCH 21, 1915. AGE AT FIRST EGG, 227 DAYS

| Date 1915–16 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | Totals | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Nov....... | | | / | | N | / | | / | / | / | / | | / | / | / | / | / | | / | / | / | / | | N | / | | / | / | / | / | ■ | 20 | |
| Dec....... | N | / | / | / | | / | / | / | | | / | | / | / | | / | | N | / | | / | | | | | | | | / | | | 13 | |
| Jan....... | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0 | |
| Feb....... | | | | | | | | | | | | | | | | | | | | | / | | / | / | | / | / | / | | ■ | ■ | 6 | 39 |
| Mar....... | / | / | / | | / | / | / | / | / | | N | / | / | | / | N | / | | N | / | / | | N | / | / | N | / | | / | | / | 19 | |
| Apr....... | / | | | / | / | / | / | | / | / | | / | | / | / | / | / | / | | N | / | | / | / | / | / | | / | / | / | ■ | 21 | |

FIG. 12. (Concluded.)

ever, have an irregular rhythm. While the observed rhythm is rarely entirely regular, yet each hen tends to produce eggs according to a rhythm that is characteristic to a certain limited degree for that individual. Superimposed on the daily rhythm are evidences of other rhythms having a beat measured by months or years. Although from another standpoint egg production is a more or less continuous process, at least in so far as the growth of the yolk is concerned, even though the fluctuations in the activity of the albumen and shell glands may be more pronounced, the rhythm may be considered as it appears on the record sheets, *i. e.*, the rhythm shown in the deposition of the eggs. Various types of rhythm have been observed. If, as a working basis, it be assumed that an egg a day represents a standard rhythm, although this high rhythm is rarely reached for extended periods, it will be found that some hens lay every other day, or we may say a one half rhythm, others two thirds, *i. e.*, two days out of three, others three fourths and so on. The three fourths or four fifths rhythm is common among most good layers. Occasionally the series may be repeated without the intervention of a zero day as is shown by the time of day the eggs are laid, for if the time of day at which the eggs are collected from the trapnests is recorded, the rhythm is shown even better than by the daily records. It has been our practise to visit the nests about every hour and a half and to record the time the eggs were gathered in units of a half hour. Thus the approximate time that each hen drops her egg is known. Rhythm, as shown by the time of day a hen lays her eggs, is an index of the essential continuity of the activities of the ovary in the growth of the ova, rather than of any rhythm in its activity, since the interval between eggs is more uniform than when the daily record only is used. One may perhaps infer that there is some rhythm in the activities of the oviduct since it is known that the stimuli for its activity comes from the presence of the yolk in its lumen. However this may

be, the several types of rhythm shown by the daily records are found to depend very much on the time of day that the eggs are laid.

None of the various types of rhythm, *i. e.,* one half, three fourths, etc., are characteristic of any one hen, although many individuals seem to center about a particular rhythm, *e. g.,* two thirds. A bird with this rhythm may fall to the one half type but does not often, except in the spring, exceed the three fourths type. While little stress can be laid on this point, it is interesting to note this tendency toward a definite rhythm in some individuals. But aside from these considerations, birds of the same age, which begin to lay at approximately the same time and which do not become broody, do not lay with the same rhythm. Thus, of two full sisters, hatched the same day, one laid only about every other day, while the second laid about five days out of six. The rhythm, then, is quite an important factor in determining the number of eggs laid.

Various causes may interfere with the normal rhythm, such as causes that interfere with the formation and growth of the egg, and other causes such as environment, season, method of management and internal factors such as broodiness. In many birds evidences of a rhythm with a period of some length may be noted as shown on page 215. The example given is of course idealized but actual records of nearly the same type may be observed.

In this connection the question of the nonproductive periods, usually of short duration, that occur in some records and which produce irregularities in the rhythm may be discussed. As will be pointed out later, broodiness is responsible for some of these periods. A similar period, that may be noted in some hens' records during the winter, may be taken as an index of the existence of a winter cycle. But other individuals may have two or more such periods or may have a single period fairly early in the winter (No. 4529, Fig. 13). Some of these periods may be inherent in the individual's makeup but

No. 4529

HATCHED MARCH 7, 1915. AGE AT FIRST EGG, 214 DAYS

| Date 1915–16 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | Totals | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Sept. | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0 | |
| Oct. | | | | | | | 7.5 | 7.5 | 9 | 9 | 10.5 | 9 | 9 | 9 | 9.5 | 1 | | 7.5 | 7.5 | 7.5 | 9 | 4.5 | | 10.5 | | | | | | | | 16 | |
| Nov. | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0 | |
| Dec. | | | | | | | | | | | | | | | | | | | | | | N4 | | | | | | | | | | 0 | |
| Jan. | | | | | | | | | | | N3 | 10.5 | | 8 | 9 | 9 | 11 | 1 | | | | 9 | 3 | | 7.5 | 10.5 | 3 | N 11.5 | 9 | 10.5 | 3 | 14 | |
| Feb. | | 7.5 | 10.5 | 3 | | 7.5 | 10.5 | 3 | | | 10.5 | 11.5 | 2 | | 7.5 | 9 | 9 | 10.5 | 10.5 | 3 | | | 9 | 10.5 | 7.5 | 9 | 10.5 | 9 | 10.5 | | | 22 | 52 |
| Mar. | 10 | | | N 10.5 | N4 | | N1 | | N1 | | N9 | | | | | N9 | N3 | | N 9.5 | N3 | | N9 | N9 | N 11.5 | N3 | N 12 | N3 | | N9 | 9 | 11 | 3 | |
| Apr. | 3 | | 7.5 | N11 | 11 | 1 | N3 | | N 7.5 | N1 | N9 | N9 | N9 | 9 | N3 | 9 | 10.5 | N 10.5 | 3 | | 7.5 | 9 | 10.5 | 10.5 | 9 | 10.5 | 9 | 10.5 | 10.5 | N 3 | | 17 | |

No. 5032

HATCHED MARCH 28, 1915. AGE AT FIRST EGG —

| Date 1915–16 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | Totals | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Nov. | | | | | | | | | | | | | | | | | | | | | | | | | | | N4 | N 7.5 | N1 | | | 0 | — |
| Dec. | N 10.5 | N 2.5 | | N 9 | N 3 | | N 10.5 | N 1 | N 4 | | N 9 | N 3 | | N 1 | N 2.5 | | N 1 | N 3 | | N 1 | | N 3 | | N 3 | | N 3 | | | | | | 0 | |
| Jan. | | | | | | | | | | | | | | | | | | | | | | | N 12 | N 1 | N 3 | | N 7.5 | N 10.5 | N 1 | N 4.5 | | 0 | |
| Feb. | N 9.5 | | | | | | | | | | | | | | | | | | | | | | | | | N 7.5 | N 12 | N 1 | N 1 | | | 0 | 0 |
| Mar. | N 1 | N 4 | | N 3 | | N 3 | | N 7.5 | N 10.5 | N 1 | N 4 | | N 9 | N 10.5 | N 1 | N 4 | | N 9 | N 3 | N 3 | | N 10.5 | N 3 | N 3 | | N 9 | N 10.5 | N 1 | N 4 | | N 9 | 0 | |
| Apr. | N 10.5 | N 12 | N 3 | | N 9 | N 10.5 | N 1 | N 4 | | N 9 | N 10.5 | N 10.5 | N 3 | | N 7.5 | N 10.5 | N 10.5 | N 10.5 | N 3 | | N 7.5 | N 9 | N 10.5 | N 3 | N 4 | N 7.5 | N 9 | N 10.5 | N 3 | N 3 | | 0 | |

FIG. 13. Types of Records. No. 4529 is that of an early maturing pullet that laid discontinuously but nevertheless made a fairly good winter record. Nos. 5032 and 246 are nesters, *i. e.*, birds that visit the nests regularly but do not lay. The time at which the egg was collected or the hen ready to leave the nest is shown by the numerals. ".5" is used for the half-hour period.

**No. 246** HATCHED MARCH 30, 1913. AGE AT FIRST EGG —

| Date 1913–14 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | Totals |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Nov. | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0 |
| Dec. | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 0 |
| Jan. | | | | | | | | | | | | | | N 3 | | N 11.5 | | N 9.5 | N 3 | | N 9.5 | N 1 | | N 11.5 | N 3.5 | | N 1.5 | | N 11 | N 3 | | 0 |
| Feb. | N 1 | | N 1 | | N 11.5 | | N 1.5 | | N 9 | N 3 | | | | | | | | | | | | | | | | | | N 4 | | | | 0 |
| Mar. | | | | N 11.5 N2 | | | N 8 | N 11.5 | N 3.5 | | N 10.5 | N 2 | | N 10 | N 1 | N 2 | | N 9 | N 1.5 | N 4.5 | | N 9.5 | N 11.5 | N 2.5 | | N 9 | N 10.5 | N 3.5 | | N 8.5 | N 10.5 | 0 |
| Apr. | N 2 | | N 10.5 | N 10.5 N2.5 | N 3.5 | | N 10.5 | N 11.5 | N2 N 3.5 | | N 10.5 | N 10.5 | N 2 | | N 8.5 | N 11 | N 2 | | N 7.5 | N 10 | N 11.5 | N 11 | N 2 | N 2 | | N 7.5 | N 10 | N 11 | N 2 | N 2.5 N4 | | 0 |
| May | | N 8.5 | N 10 | N 10 | N 2 | N 2 | | N 8.5 | | | N 2 | | N 8.5 | N 10 | N 11.5 N2 | N1 N3 | | N 8.5 | N 10 | N 11.5 | N 11.5 | N 3.5 | | N 9.5 | N 10 | N 2 | N 2 | | N 8 | N 11.5 | N 2 | 0 |
| June | | N 8 | N 10 | N 11.5 | N 1.5 | | N 10 | N 10 | N 10 | N 11.5 | N 1.5 | | N 1.5 | | N 2 | | N 8.5 | N 10.5 | N 2 | | N 10 | N 11.5 | N 2 | N 8.5 | N8 N 10 | N 11.5 | N 1.5 | | N 8 | N 10 | | 0 |
| July | N 10.5 | N 11.5 | N 2 | N 3 | | N 8.5 | N 10.5 | N 2 | | | | | | | | | | | | | | | | | | N 7.5 | | N 11 N2 | | N 1.5 | | 0 |
| Aug. | N 8.5 | N 12 N 2.5 | | N 11 | N 4 | | N 8.5 | N 11 | N 2.5 | | N 8.5 | N 10 | N 4 | | N 8.5 | N 12 | N 2 | N 8.5 | N 11 | N 10.5 | N 1.5 | N 4 | | N 8.5 | N 11 | N 1.5 | | N 10 | N 11.5 | N 3.5 | | 0 |
| Sept. | N 9 | N 11.5 | N 3.5 | | N 10 | N 1.5 | | N 10 | N 2.5 | N 4 | | N 8.5 | N 12 | N 3 | | N 10 | N 4 | | N 8.5 N 11.5 | N 1 | N 3.5 | | N 9.5 | N 1.5 | | N 11.5 | N 4 | | N 10.5 | N 1.5 | | 0 |
| Oct. | | N. 11 | | | N 11.5 N1 | | N 11.5 | | N 1.5 | | | | | | | | | | | | | | | | | | | | | | | 0 |

FIG. 13. (*Concluded.*)

Years' Total 0

others are probably the result of the environment, since it is well known that nonproductive periods can be induced by artificial means.

One of the most interesting things in connection with the rhythm of egg production as observed by Pearl ('12) is the existence of hens which never lay an egg, but the record of whose visits to the nests shows a very definite rhythm. A number of such hens have appeared in our flocks. (Nos. 5032 and 246, Fig. 13.) The hour of their visits to the nest exhibits exactly the same sort of rhythm as normal hens. These facts point strongly to the existence of some mechanism other than the formation and deposition of an egg which controls the extrusion of the egg. It is interesting to note that if one of these hens is removed from the nest before she is ready to leave, she returns and persists in doing so until, shall we say, she thinks she has laid her egg. Autopsies of several of these hens show that they fall into two classes; viz., those that are producing yolks or eggs but depositing them in the abdominal cavity, and those in which a tumor of the reproductive system is involved.

*Laying hens* often visit the nest at the proper day and hour but fail to lay. Such hens (No. 4529, Fig. 13) usually lay the day previous and the day after in regular routine, though at times they may pay two or more such nonproductive visits in succession.

A study of these latter records shows that some hens have indications of a potential capacity greater than the actual capacity revealed in the records. Very many hens pay an occasional visit to the trap nest without laying (note the *n*'s in the various records), while a few pay such visits more or less regularly, at various periods of their lives. The striking feature of these visits is that they are made at the hours one would expect if an egg were actually laid (No. 4529, Fig. 13), though the nature of the stimulus that causes such visits is uncertain.

*Broodiness.*—Broodiness, from the commercial as well as biological standpoint, is one of the most important of

the factors influencing egg production. In general, with the onset of the first broody period, the monthly production falls off 40 per cent. of its former rate. Broodiness, however, as met with in the laying hen, is to some extent an artificial condition. In a free state a hen becomes broody after she has laid a clutch of eggs, incubates them, and rears a brood of chickens. Altogether she is not producing eggs for a period of some ten weeks or more. After this she may again lay a clutch and repeat the process. Egg production under such conditions remains at a relatively low ebb. It is a matter of common knowledge among poultry keepers, however, that by various means the broody hen can be "broken up." That is, she can be induced to discontinue manifestations of broodiness and after a period varying from a few days to several weeks will begin to lay again. As a rule, however, only a few—ten or twelve—eggs are laid before a hen goes broody again. The process may be repeated indefinitely.

There is a considerable variation in the number of times a hen goes broody in a year, the length of the broody periods, the trouble required to break her up and other characteristics of broodiness.

The age at which the first broody period occurs depends in part upon the time a hen begins to lay. In the vast majority of instances egg production precedes broodiness. At least 15 to 20 eggs are laid before a hen becomes broody, though it may be many times that number. *Age incidence* in the first place depends upon the age at which the hen lays her first egg but after that it depends upon other circumstances, which have not been determined. Thus, the age of a bird at her first broody period may vary from eight months up to the end of the second year. Usually, however, the first broody period comes on when the bird is from 11 to 15 months of age. After the first broody period, the periods recur about once a month, if the hen is promptly broken up. There are records in our files of a few Rhode Island Red hens

that have not been broody for from one to three laying years.[5]

The number of broody periods per year, then, depends upon the date of the first period and in the second place upon the cessation of production in the fall. Egg production usually, but not always, ceases with a broody period.

A broody period has two phases. First, the period of manifestations of broodiness such as clucking, ruffling of feathers and cessation of production. This period is variable, some hens being easy to "break up" while others are very difficult. Manifestations of broodiness sometimes begin several days before egg production ceases, and may rarely continue without cessation of egg production or without hanging to the nest. I do not recall a case when egg production began before the cessation of the manifestations of broodiness.

The second phase begins with the disappearance of the manifestations of broodiness, and extends up to the time egg laying recommences. Its chief characteristic is nonproductiveness and its length varies considerably.

Broody periods coming during the height of production, March and April, are usually of short duration, but gradually lengthen as the summer advances, until they sometimes last for a month or more. During the winter months, the periods are longer than those occurring during the spring and often lead to the cessation of egg production for several months.

Egg production is affected by broodiness chiefly through the number of broody periods. Hens that go broody many times during the year have a much lower production than others that go broody only two or three times, other things being equal. It is of particular interest to note the abrupt way in which the monthly egg production usually decreases with the onset of broodiness, regardless of the time of the year. Thus, a hen

[5] The statements in this section are based on an intensive study of broodiness, the data on which will be published in due course of time.

may be laying at a 75 per cent. rate before going broody, but with the appearance of the first broody period production falls off 40 per cent. of its former rate. In general it has been found that for each hen the rate for the broody part of the year is only about 60 per cent. of the rate of the nonbroody part.

It is not known whether the intense development of broodiness in the summer months is directly due to the weather conditions as such or whether it is due to some internal cause or is part of the annual cycle. At any rate it is evident that it operates to decrease the egg production very considerably. Further discussion will be postponed until the study of broodiness now in progress is ready for publication.

*Types of Winter Records.*—The various factors described in the foregoing pages combine in many ways and produce as a result different types of records, several of which may now be discussed in more detail. For the present we may divide the various types of records into high (over 30 eggs), mediocre (under 30 eggs) and zero producers.

High producers (over 30 eggs) may be divided into several subclasses. First, the early maturing, nonbroody high that lays continuously at a high rate and makes a very high record (No. 4846, Fig. 3). Second, the late maturing nonbroody high that lays continuously at a high rate but makes a lower record than the first in direct proportion to the difference in maturity. (See Figs. 3 and 4.) Third, the broody, early maturing high that lays at a high or fairly high rate during the laying periods (not shown). Such a bird's record is cut very materially by the broody periods. Individuals of this type are not very numerous during the winter period. Fourth, there is the high bird that exhibits a pronounced winter cycle or period of good production during the early part of the winter, but which stops after a time and may not lay at all for several weeks. This type is closely related to the bird that lays her eggs in clutches, but because of her

early start makes a comparatively high record. Finally there is the type of bird shown by No. 4797, Fig. 11, that matures early, lays steadily and does not go broody but lays at a comparatively slow rate. Such birds may make high records, but they never make the highest ones.

Mediocre producers (under thirty eggs) may result from any one of the various types previously described for high producers through the failure of one or more factors. Thus, delayed maturity will cause a bird to fall below the dividing line at 30 eggs to a degree that will vary inversely with the age at first egg, due allowances being made for the date at which the individual was hatched (Fig. 4). Or a bird may fall below the required number of eggs through a slow rate of production (No. 5080, Fig. 11, or Nos. 224 or 284, Fig. 12). The former type of bird (Fig. 4) would seem to be a late maturing high, since it is clear that its record results directly from the variability in time of first egg. Hence this type of mediocre producer is to be regarded as an artificial class rather than a real class as in the case of the birds typified by No. 5080.

Zero producers, by definition, are birds that do not lay until after March 1, and need no further discussion, except to note that some of them clearly result from the combined effects of date of hatch and age at first egg rather than from an inherent inability to lay during the winter (*i. e.*, from a lack of the winter cycle).

There are, then, numerous types of records resulting from the interaction of the various components described in the earlier part of the paper. Although the records described are winter records, the observations apply equally to annual egg production. High egg production results only from a combination of the right set of factors. If any one of several of these factors fail, egg production is lowered.

*(To be concluded.)*

# BACTERIAL PHYLOGENY AS INDICATED BY MODERN TYPES[1]

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THE importance of the group we call bacteria in any theories concerning the origin and evolution of life on our planet is well shown by several recent writers on the subject, notably Jensen (1909), Osborn (1916), and Kligler (1917). In each case, however, there are certain misinterpretations of our knowledge of the modern bacteria and their function which go far to invalidate, or at least to weaken, the specific conclusions which they reach with reference to the types of primitive bacteria.

In our search for hints as to ancestral types by investigation of modern species of bacteria we must hold in mind that although present-day bacteria approach most closely to what we conceive must have been primitive life, nevertheless and for this very reason the group of modern bacteria must have the longest evolutionary history of any existing group. That any modern species closely resembles the original type is therefore not extremely probable. It can not be too often emphasized that in speculations concerning evolutionary history based upon modern forms with no adequate fossil ancestral types we must deal only with the tips of the ultimate twigs of the branches of the evolutionary tree. By a careful comparison of the surviving forms we may gain a knowledge of their probable relationships, but it should be remembered that in no case this relationship is that of parents and offspring, but that of brothers and cousins. Perhaps we may speculate upon the probable arrangement of the branches of the evolutionary tree that have disappeared

[1] From the Bacteriological Laboratories.

in past geologic ages by study of the survivors, but it is self-evident that there should be a perfect knowledge of these survivors, morphological and physiological, so that we may not be led astray by superficial resemblances when there exist, in fact, deep-seated and fundamental distinctions.

The geologic evidence that has been adduced as to the character of the primitive bacteria is of but the slightest value. Speculation as to the primitiveness of nitrogen fixers, for example, based upon the geologic evidence introduced is scarcely convincing.

It should also be noted that it is quite possible that the bacteria do not constitute an homogeneous group in the sense that all are descended from a single primitive type of bacterium. It may be that there have been included in the group bacteria forms which have assumed similar morphological or physiological characters without having a common ancestry. Botanists, for example, at the present day are by no means convinced that seed plants have all had a common origin; in other words, the ability to produce seeds may have arisen independently in two or more groups of the fern plants. It is possible that some of the forms we term bacteria have been derived from the fungi, others from the blue-green algæ or possibly some even from the protozoa. In short, it may be that the actual relationships existing between various bacteria may be very distant.

A study of these modern bacteria will reveal relationships such as those just indicated. The possibility that the bacteria are a derived group must be constantly held in mind. To prove that they are primitive it must be shown that no group from which they might have sprung or to which they seem to be related can be regarded as more primitive. This has not been satisfactorily accomplished in certain cases.

Modern systematic bacteriologists are in fair agreement that there should be recognized five or six distinct groups or orders of bacteria. Of these, the *Eubacteriales*,

or true bacteria, are generally regarded as the least specialized and possibly the most primitive. It is possible that the great group of the sulphur bacteria, the order *Thiobacteriales,* is equally primitive, though the genera and species have been less studied and are not as well known. There are unquestionably many intergrading forms between the *Eubacteriales* and the *Thiobacteriales,* as shown by close parallel series of morphological types. It seems equally clear that there are intergrading forms between the *Thiobacteriales* and the blue-green algæ. Morphologically, too, one may find every gradation between the typical colorless, sulphur-containing *Beggiatoa,* through species of this genus showing bacteriopurpurin, through the faintly colored, slender *Oscillatoria* to the thick, deeply pigmented forms. If these intergradations and indicated relationships are real, it is apparent that the true bacteria may have come from the blue-green algæ through the sulphur forms, or the blue-greens may have come from the true bacteria, or the sulphur forms may be closer than either of the other groups to the primitive types from which all three groups have been derived. While there is no definite proof apparently possible at the present time, it is not at all improbable that the last assumption is the true one. A relationship quite certainly exists between the group of sheathed filamentous bacteria (the *Chlamydobacteriales*) and the blue-green algæ. The resemblance is so well marked that certain species of the iron bacteria are quite commonly included by algologists among the algæ. The relationship to the *Eubacteriales* is not quite so clear. Possibly the genus *Sphærotilus* (*Cladothrix*) may be regarded as a link, for this organism consists of rod-shaped cells occurring in chains, all embedded in a gelatinous sheath. Motile cells (gonidia) with polar flagella somewhat resembling *Pseudomonas* types may be developed.

The fungi apparently are related to certain of the bacteria through the *Actinomycetales.* This latter group has some resemblance to certain of the true bacteria such

as the *Lactobacillus* of sour milk and the diphtheria types. It is possible that these organisms together with a few genera from the *Eubacteriales* represent an entirely distinct series. The *Spirochætales* apparently constitute a group showing combinations of characters which relate them to the *Eubacteriales* and the *Thiobacteriales* on the one hand, and the *Protozoa* on the other. The group *Myxobacteriales* is apparently related to the true bacteria, but not to higher groups of plants or animals, unless there may be some as yet undiscovered relationship between these forms and the slime molds as suggested by a superficial study of their fruiting forms.

The interrelationships just discussed among the various great groups of bacteria may be illustrated by the following diagram in which the connecting lines are intended to show relationship, but not necessarily derivation.

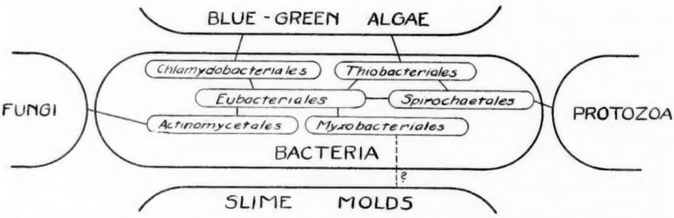


FIG. 1. CHART ILLUSTRATING THE PROBABLE INTERRELATIONSHIPS OF THE GREAT GROUPS OF BACTERIA AND THEIR RELATIONSHIPS TO OTHER GROUPS, as Fungi, Blue-green Algae and Protozoa.

From the standpoint of the student of evolution the order *Eubacteriales* (possibly also *Thiobacteriales*) is of special interest, for within it is probably to be found greater variation in physiological activity than in any other group of plants or animals. A comparison of the modern forms belonging to this group may well give some hint as to their evolution. Too much can not be expected, however, without getting far into the realms of speculation.

After rather careful consideration a committee of the Society of American Bacteriologists has proposed a list

of names to be recognized as valid for the genera of this order. They have also suggested that these genera be grouped in seven families. Altogether twenty-eight genera are recognized. It should be possible, if adequate knowledge is at hand, and the *Eubacteriales* constitute an homogeneous group, so to arrange these genera as to show their probable and their possible relationships, and perhaps gain some knowledge thereby of their origin and evolution.

From the standpoint of the evolution of bacteria we are much interested in the organisms which can live and grow in the total absence of organic matter, those which utilize inorganic substances exclusively in the manufacture of their own food, in short, those bacteria which are strictly prototrophic.

Let us consider the possible sources of the various elements needed in the building up of the primitive bacterial protoplasm. We have no reason to suppose that such primitive bacterial protoplasm differed in any marked degree from the protoplasm of modern forms. Such organisms must have available carbon, hydrogen, nitrogen, oxygen, sulphur, phosphorus and iron, with small quantities of a few other elements. Upon the earth before the advent of other plant life, the carbon necessary for growth would probably be secured from carbon dioxide, or possibly from methane or carbon monoxide; the hydrogen was undoubtedly present in abundance in water, perhaps traces also of the free element, of methane, or of ammonia may have been available; the nitrogen was probably present in sufficient quantities either as ammonia or as nitrates, and of course in the form of less available, relatively inert, gaseous nitrogen; the sulfur probably existed as sulfids, sulfates, and free sulfur; the phosphorus was probably found in phosphates and the iron in both ferrous and ferric condition. It is evident that elements and compounds were present in abundance and variety, but not in the form of *organic* compounds. All modern living organisms are divided into those which

require their food to be ready manufactured for their use, and those which can manufacture their own food (prototrophic). It is apparent that the primitive organism was probably prototrophic.

The manufacture of food from inorganic materials requires the expenditure of energy. We must account, if possible, for the sources of such energy for the prototrophic forms. Among modern organisms the energy needed is secured always from one of the two sources, light rays or chemical oxidation. While other types of energy are known, apparently plants have not been adapted to their utilization. If light rays were first used as an energy source, the primitive organism was probably provided with some pigment which was of significance in the absorption of the light and in its conversion into chemical energy. Among modern forms which may have resembled such primitive organism may be cited the simpler types of the blue-green algæ and the phototactic sulphur bacteria containing the pigment bacteriopurpurin. If the Chamberlin planetesimal hypothesis of earth origin is accepted, such might very possibly have been the primitive types. However, primitive conditions may have been such that light energy was not available. Organisms developing under such conditions must have been directly dependent upon chemical energy. Such energy might be secured by the oxidation of ferrous iron, of free sulphur or of the sulfids (particularly hydrogen sulfid), methane, hydrogen, carbon monoxid and ammonia. Organisms among modern species are known which can utilize each of these methods of securing energy. There is no reason, therefore, why any one of these should not be a method used by a primitive form. The modern types of organisms which oxidize ferrous to ferric iron are in many respects among the most highly differentiated of the filamentous bacteria and show many points of resemblance to the blue-green algæ. They show few primitive characters, and are probably to be regarded as not closely related to the primitive bacteria.

A study of the organisms which at the present time are known to secure energy by the oxidation of $H_2S$, $CH_4$, $H_2$, $CO$ and $NH_3$ show that they possess certain characteristics in common. For the most part the organisms are cocci or rods, occasionally spiral, in some cases motile, and then always with polar flagella. While there are some exceptions to the rule, the organisms for the most part do not thrive in a medium containing much organic matter. It is not improbable that the primitive organism had characters not greatly unlike these enumerated. Just what type of oxidation is most primitive it is difficult if not impossible to determine, although certain conjectures may not be out of place. Probably one of the most common of the easily oxidized substances of the primitive earth was hydrogen sulfid. It undoubtedly was a common constituent of thermal springs. The modern representatives of the groups which thrive in water containing hydrogen sulfid are abundant both in numbers and in species. By means of the energy which they secure from the oxidation of $H_2S$ and S they probably take up $CO_2$ and transform it into food and protoplasm. Apparently all of the forms which have been investigated are motionless cocci or rods or spirals motile by means of *polar* flagella. No modern form is known which produces spores. Many of the species contain a pigment bacteriopurpurin and swim or grow toward light, showing positive chemotaxis or chemotropism. We may find every gradation between the modern representatives of these forms and the blue-green algæ, on the one hand, and the true bacteria, on the other. Many of the blue-green algæ contain a purple coloring material in addition to the blue and green pigments. From the standpoint of evolutionary requirements, therefore, it is evident that some primitive organism having much the same type of metabolism as the modern sulphur bacteria would be a satisfactory starting form.

Before additional stress is laid upon a sulfur bacterium as a possible progenitor of modern forms, we

should examine carefully other possibilities. It is conceivable (though scarcely probable) that hydrogen may have constituted a larger percentage of the atmosphere in times past than now. Several species of modern bacteria have been described which in the presence of hydrogen and oxygen may secure their growth energy by combining these elements directly or indirectly. These species are motile rods with *polar* flagella. These modern members of the genus *Hydrogenomonas,* however, are very far from primitive because under ordinary conditions they are pantotrophous growing well on ordinary laboratory media. Thus far no organism strictly prototrophic capable of utilizing hydrogen has been found. This does not prove that such organism has not existed, but throws the burden of proof upon any one who would urge hydrogen oxidation as a primitive method of securing growth energy. The results of Kaserer (1906) seem to indicate that the organism catalytically causes the transformation in the presence of hydrogen of carbonic acid into formaldehyde, the cell then using the formaldehyde as food.

Methane and carbon monoxide are also oxidized by certain of our modern bacteria, the organisms securing their growth energy in this manner. These organisms according to the descriptions are autotrophic and do not thrive in the presence of organic material. It is possible that these represent primitive characters. The organisms are rods, motile or non-motile, when motile with *polar* flagella. If either methane or carbon monoxide were common in the atmosphere of the early earth, forms of this general type may have flourished. That these gases were sufficintly abundant does not seem probable, but the possibility must be admitted.

Several types of modern bacteria are known which oxidize ammonia to nitrites and nitrites to nitrates, utilizing the energy thus secured for chemosynthesis of food from inorganic materials. At least one species of the nitrifying bacteria is a coccus, others are rods, motile by

means of polar flagella. It is not at all improbable that ammonia may have been abundant enough on the primitive earth to have constituted an adequate energy source for the primitive bacteria.

Which of these modern types most closely resembles the primitive organism living on autotrophic existence? It is perhaps impossible to say. The modern representatives of the nitrifiers and the methane and carbon monoxid oxidizers are apparently rather isolated groups without numerous species and apparently not closely related to other forms. The sulfur oxidizers, on the other hand, are abundant, of many types, and show many intergradations with other bacteria and the blue-green algæ. Possibly a somewhat better case can be made out for them. However, it should be noted that all of these forms have certain characters in common, they are all autotrophic, all are aerobic, and when motile are elongate cells with polar flagella. It is perhaps a fair inference that the aerobiosis and the polar flagellation are primitive characters. We may well conclude with Jensen that all of these organisms discussed are related and may be

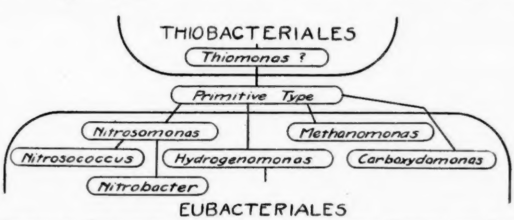


FIG. 2. PROBABLE RELATIONSHIP OF CERTAIN MODERN GENERA OF BACTERIA TO THE PRIMITIVE ORGANISM AND THEIR RELATIONSHIPS TO EACH OTHER.

placed in a single group. Expressed in terms of modern representatives of the primitive types, the following diagram might express the idea.

We may next concern ourselves with possible and probable relationship of these various forms to other members of the *Eubacteriales,* disregarding the *Thiobacteriales.* The remainder of the *Eubacteriales* differ from the autotrophic forms thus far discussed in that in

every case they require the presence of organic carbon compounds in the substrate in which they grow. These compounds may be of the greatest diversity of types, but none of the bacteria are capable of manufacturing their own carbon food. It is possible that other types of bacteria than the prototrophic may not have developed upon the earth until after the evolution of higher plants, such as the algæ, upon which they could depend for food. Possibly there may have been some start made, however, in the utilization by one type of organism of the dead bacterial protoplasm of another type.

How may we detect relationships of modern metatrophic bacteria to these more primitive types? Possibly by a study of intergrading forms. The genus *Hydrogenomonas* apparently is either autotrophic or metatrophic according to the conditions of the environment. Some primitive organism may have acquired properties similar to those of the modern *Hydrogenomonas* and constituted the progenitors of the modern forms. Possibly this type of differentiation may have arisen in several groups. It is conceivable, for example, that some organism having characters such as *Nitrosococcus* might have given rise to an independent branch, possibly to forms like *Micrococcus*. This, of course, is pure speculation.

Among the metatrophic bacteria we are probably justified in placing the genus *Pseudomonas* as most closely related to the forms discussed because of its close morphologic resemblance, with rod-shaped cell and polar flagella, to the autotrophic forms; then too, there is the evidence of the intergrading *Hydrogenomonas*. Somewhat less diversified in nitrogen metabolism are the related genera *Azotabacter* and *Rhizobium*, both usually with polar flagella, rod-shaped bodies, primitive nitrogen requirements, and marked capacity to utilize carbohydrates, oxidizing them quite completely to $CO_2$ and $H_2O$. The supply of energy is so abundant to these organisms that in the absence of sufficient combined nitrogen in the substrate they can fix atmospheric nitrogen, and build it into their protoplasm.

This nitrogen fixation must be carefully differentiated from the nitrification previously discussed. Probably the non-motile group *Mycoderma* which resembles the other organisms in ability to oxidize sugars (preferably ethyl alcohol), but is non-motile, should be placed here. These three genera are obligate aerobes and secure their growth energy by relatively complete oxidation of carbohydrates, alcohol or even acetic acid. They apparently constitute a natural group related to *Pseudomonas.* It should be recalled that a statement of relationship does not imply derivation, but simply common ancestry.

We have now considered all the bacteria which show the primitive characters of polar flagellation and obligate aerobic utilization of carbonaceous foods. In the genus *Pseudomonas* we find evidences of differentiation in metabolism, particularly ability to bring about proteolysis. In some species we have evidences of adaptation to anaerobic conditions, among the so-called denitrifiers. Some members of this group are capable of taking oxygen from nitrite and nitrates under anaerobic conditions, with evolution of free nitrogen. Other forms are known that can reduce sulfates to sulfids. Such facultative anaerobes, securing oxygen from an easily reduced compound, evidently make use of the oxygen in the same manner as though growing under aerobic conditions for the oxidation of carbon compounds. The next step in the development of anaerobiosis was probably the utilization of carbon compounds, securing growth energy by intramolecular oxidations; in such forms fermentative capacity becomes well marked.

The close relationship in morphology and physiology existing between the short spiral *Vibrio* and *Pseudomonas* indicates that the family *Spirillaceæ* has come from an ancestry having much in common with *Pseudomonas.*

The other bacteria belonging to the *Eubacteriales* are more specialized in general morphology and in physiology than the forms thus far mentioned. When motile the cells are peritrichous rather than with polar flagella.

Some forms have developed the ability to produce endospores (family *Bacillaceæ*) and seem to comprise a closely related group of genera whose relationship to the more primitive types is somewhat problematic. Another well-marked group of bacteria includes the large series of (usually) gram-negative bacteria that produce no spores. These may be included in a family *Bacteriaceæ*. With the exception of polar flagella, there is no very marked difference between the *Pseudomonas* forms and the *Proteus* types. It is quite possible that they are closely related. The cocci apparently form another homogeneous group, the *Coccaceæ*. The affinities of the group may be sought in several places. For example, there is apparently very close resemblance culturally and physiologically between the chromogenic cocci and the chromogenic rods closely related to the genus *Bacterium;* the organism usually termed *Bacillus prodigiosus* (*Serratia marcescens*) is remarkably near certain red cocci as *Rhodococcus roseus*. The possibility that there is a relationship between the *Nitrosococcus* and *Micrococcus* has already been pointed out. Then there is a decided relationship evident between the aciduric bacilli and the genus *Streptococcus*. All of these origins are possible; if all these relationships are true, the group *Coccaceæ* must be regarded as heterogeneous, that is, polyphyletic.

The group containing the tubercle bacillus (*Mycobacterium*) and diphtheria bacillus (*Corynebacterium*) shows undoubted relationships to the order *Actinomycetales*. If they have no common origin with other genera of the *Eubacteriales* they should be included in the order *Actinomycetales*. However, there is decided evidence of relationship through *Leptotrichia* and perhaps *Erysipelothrix* to the lactic acid bacteria. If this is a valid relationship it would indicate that the *Actinomycetales* are an offshoot of the *Eubacteriales*, or at least have a common ancestry.

The various relationships illustrating the probable phylogeny of the class Bacteria is illustrated in the ap-

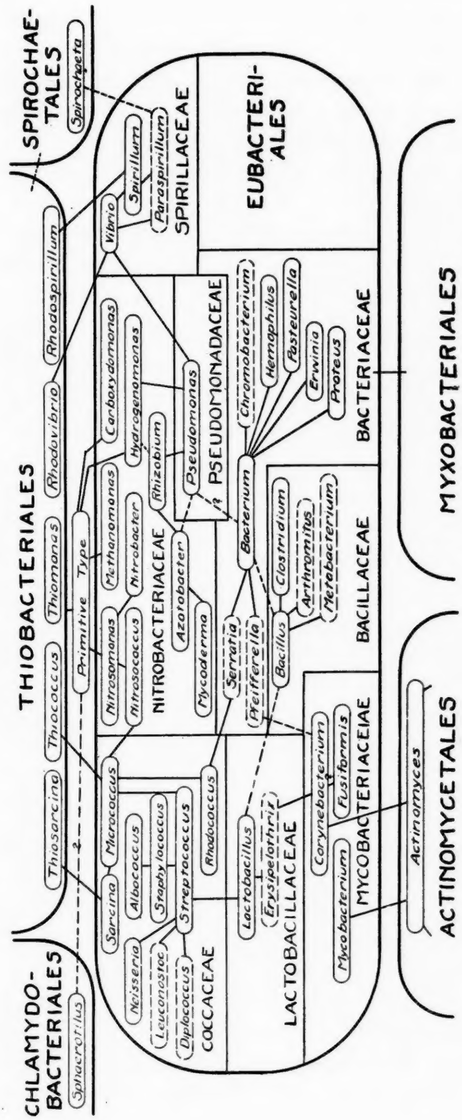


Fig. 3. Suggested Interrelationship of the Genera, Families and Orders of Bacteria.

pended diagram. Relationships which have appeared probable to the writer have been indicated by solid lines connecting genera, possible relationships have been indicated by dotted lines. The genera comprising the families recognized by the Committee on Nomenclature as belonging to a single family are enclosed by a heavy line. Genera not recognized by the committee are enclosed in dotted lines.

The foregoing analysis would seem to indicate that the grouping of genera by the Committee on Classification, with some slight modifications possibly, represents fairly well true phylogenetic relationships of the bacteria. The exact boundaries of the families are of course of little importance providing the scheme of classification tends to show relationships.

# DISPROOF OF A CERTAIN TYPE OF THEORIES OF CROSSING OVER BETWEEN CHROMOSOMES[1]

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## I

Two types of relations have been proposed to account for the facts of "crossing over" between pairs of characters that follow the same pair of chromosomes. One is a varying relation between the substances forming the factors belonging to *diverse pairs* in the same chromosome; the other a varying relation between the *two members of the same pair,* in the two paired chromosomes.

The former type is represented by the "chiasmatype" theory, held by Morgan and his associates, in which the diverse relations are held to be, or depend upon, the actual diverse distances apart of the factors extended along the linear chromosome. When the chromosome breaks, for any cause, it is more likely to separate two factors far apart than two close together; on this depends the varying cross-over ratios.

The second type is that brought to notice recently by Goldschmidt (1917), and commonly called the "variable force" theory. It is conceived that the two members of a given pair, as A and a, in the two paired chromosomes, may be held or drawn to their places by a pair of varying forces, which allow them to exchange places on the average in a certain proportion of cases; while B and b are held by a different pair of forces, which allows these two to interchange in a different proportion of cases; C and c by a still different pair, etc. The result would be diverse

[1] This paper arose and took shape during discussions on theories of crossing over in the Seminary on Genetics at the Johns Hopkins University.

ratios of crossing over when diverse pairs are compared; the cross-over ratio between A–a and B–b would be different from that between A–a and C–c, and so on. It is this theory that I propose to examine. I do not understand that Goldschmidt commits himself to any form of this theory, or to any theory that is exclusively of this type, so that this discussion is not presented as a commentary on his views, but on this type of theory for its own sake. Is it possible to explain the observed ratios of crossing over by any theory of this type?

To grasp the matter clearly, it will help to have an example before us. Let the following twelve groups of letters represent twelve pairs of chromosomes in twelve cells, each chromosome bearing two factors, which we will call A–B and a–b. The upper two letters in each pair show a single chromosome containing the factors A–B, the lower two the mated chromosome containing the factors a–b.

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| I. | AB | AB | A*B* | *A*B | AB | A*B* | AB | *A*B | A*B* | AB | AB | *AB* |
| | ab | ab | a*b* | *a*b | ab | a*b* | ab | *a*b | a*b* | ab | ab | *ab* |

Now suppose that the forces holding A and a to their chromosomes are such that A and a exchange in one fourth of all cases, while B and b exchange in one third of all cases. That is, A and a exchange places in every fourth chromosome pair, B and b exchange places in every third pair. The letters that are thus to exchange with their mates are italicized in the pairs indicated above. The exchanges will evidently give the following result:

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| II. | AB | AB | Ab | aB | AB | Ab | AB | aB | Ab | AB | AB | ab |
| | ab | ab | aB | Ab | ab | aB | ab | Ab | aB | ab | ab | AB |
| | | | + | + | | + | | + | + | | | |

By a cross-over is meant the fact that two factors of diverse pairs, as A and B, which in the germ cells that formed the parent were following the same chromosome (as in I, above), are found in the germ cells *from* those parents (II, above) to be following diverse chromosomes (as in the third pair of II, above); while conversely the two factors A and b, which were following diverse

chromosomes, are now following the same one. The cross-overs in II, above, are those indicated by the + sign; there are five of these. The ratio of the number of these new combinations (5) to the total number of germ cells (12) is the cross-over ratio; in this case the cross-over ratio is $5/12$, or .417.

Examination of this case will illustrate an important fact. *A cross-over is produced only when one of the two pairs exchanges while the other does not.* In the last pair to the right, in the example given above, the members of both pairs exchange places, but this does not give a cross-over—since A and B are still together, as they were before the double exchange.

Now if the number of exchanges for each pair of cells is different from that in the example given above, the resulting cross-over ratio will be different. By supposing each pair of factors, A–a, B–b, C–c, D–d, etc., to have its own characteristically diverse frequence of interchange of its members, all sorts of cross-over ratios could be obtained, varying from 0 to 1; that is, from no cross-overs to all cross-overs. The question in which we are interested is, could the observed cross-over ratios in such an organism as *Drosophila* be accounted for in this way?

It is to be noted that the problem as we take it up is independent of the nature of the forces that hold A and a (and the other factors) in their places, and that permit them to exchange in a certain proportion of cases. These forces may be utterly heterogeneous in the different cases; they may turn out to be of any kind whatever, so far as this examination goes. We ask merely whether, if the forces, whatever they are, give a constant average proportion of interchanges characteristic for each pair, they can yield the cross-over ratios actually observed.

## II

It is evident that on this theory there are two kinds of ratios to be dealt with: the ratio of the number of interchanges of A and a (characteristic for each pair), and the ratio of the number of cross-overs, between two pairs A–a

and B–b; the latter of these ratios depends on the former. We shall call the former the exchange ratio; the latter is commonly known as the cross-over ratio, which we will designate by the letter C.

The exchange ratio signifies the ratio of the number of exchanges between A and a to the total number of germ cells:

$$\text{Exchange Ratio} = \frac{\text{Exchanges}}{\text{Total Number}}$$

The cross-over ratio (C) signifies, of course (following Morgan and the general usage), the ratio of the number of cross-overs to the total number of germ cells or progeny:

$$C = \frac{\text{Cross-overs}}{\text{Total Number}}$$

Goldschmidt (1917, page 90) has given a formula for the cross-over ratio resulting from any two exchange ratios, and has computed the resulting cross-over ratios from certain assumed exchange ratios. We shall give the formula a simpler expression than Goldschmidt has done; one that will enable us to determine its properties and limits of performance.

In cross-over ratios we deal with two pairs of characters, which we may designate A–a and B–b. Let $x$ signify the exchange ratio for one of the pairs; and let $y$ signify the exchange ratio for the other pair. Thus, if $A$ and $a$ interchange in one third of all cases, this pair's exchange ratio x will be one third (or .33⅓); while if $B$ and $b$ interchange in two fifths of all cases, its ratio, $y$, will be two fifths (or .4). For convenience we will always choose $x$ and $y$ in such a way that if there is any difference, $x$ will designate the smaller ratio. That is, $x$ will always be equal to or less than $y$.

Now, suppose that originally the first chromosome of the pairs bears the two factors A and B, the second a and b (as in I, above). After crossing over in the proportion

x, we shall have, in these first chromosomes of the pair, A and a in the following proportions:

$$xa$$
$$(1-x)A$$

Similarly, in this same chromosome we shall find *B* and *b* distributed in the following proportions:

$$yb$$
$$(1-y)B$$

(Thus, if A and a interchange in two fifths of all cases, then after interchange we shall, in the first chromosome, find *a* in two fifths of the cases, A in three fifths; and similarly for B.)

What will then be the proportions of the various combinations of the two pairs of factors? It will evidently be

$$\begin{aligned} &xa + (1-x)A, \text{ multiplied by} \\ &\underline{yb + (1-y)B} \\ &= xyab + x(1-y)aB + y(1-x)Ab \\ &\qquad + (1-x)(1-y)AB \end{aligned}$$

The cross-overs are aB and Ab, the proportion of which is evidently:

$$x(1-y) + y(1-x) = x + y - 2xy$$

The same result will be reached if we consider the second chromosome of each pair (that which originally contained *a* and *b*); so that the same proportion holds for both together. This, therefore, gives us our formula for the cross-over ratio in terms of the exchange ratios of the two pairs. It is essentially the same formula employed by Goldschmidt (1917), giving the same results, but written in more perspicuous form.

Let us therefore recapitulate in algebraic form the essential points.

Let

$$x = \text{exchange ratio of one pair,}$$

$$y = \text{exchange ratio of other pair}$$

$$(\text{so selected that } x \gtreqless y).$$

Then for the cross-over ratio (C) of the two pairs, the formula is

$$C = x + y - 2y.$$

An example or two will make the use of this formula clear. Suppose that the exchange ratio of pair A–a is $3/7$; of B–b it is $2/5$. Then

$$x = 2/5; \qquad y = 3/7$$

$$C = 2/5 + 3/7 - 2(2/5.3/7) = 17/35 = .486$$

Again, let

$$x = .31, \qquad y = .34$$

$$C = .31 + .34 - 2(.31 \times .34) = .439$$

(It is customary to express the results as percentages; thus the last example would give a cross-over ratio of 43.9 per cent. For our purposes it is more convenient to leave them as decimals.)

Now this formula has certain characteristics and limitations that allow us to bring the theory on which it is based to a test. The theory is that each pair has its characteristic exchange ratio; if that be the case, this formula holds.

We shall set forth certain of the important relations between cross-over ratio and exchange ratios, revealed by this formula; then show how these provide a test for the theory which the formula expresses. To aid in the comprehension of these relations, we give a table showing all cross-over ratios for two pairs of characters, resulting from the combinations of exchange ratios varying by tenths from 0 (no exchange) to 1 (all exchange). The table illustrates all the relations to be deduced from the formula.

Exchange Ratio for One Pair (A–a).

| Exchange Ratio for the Other Pair (B–b). | 0 | .1 | .2 | .3 | .4 | .5 | .6 | .7 | .8 | .9 | 1.0 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| .0 | 0 | .10 | .20 | .30 | .40 | .50 | .60 | .70 | .80 | .90 | 1.00 |
| .1 | .10 | .18 | .26 | .34 | .42 | .50 | .58 | .66 | .74 | .82 | .90 |
| .2 | .20 | .26 | .32 | .38 | .44 | .50 | .56 | .62 | .68 | .74 | .80 |
| .3 | .30 | .34 | .38 | .42 | .46 | .50 | .54 | .58 | .62 | .66 | .70 |
| .4 | .40 | .42 | .44 | .46 | .48 | .50 | .52 | .54 | .56 | .58 | .60 |
| .5 | .50 | .50 | .50 | .50 | .50 | .50 | .50 | .50 | .50 | .50 | .50 |
| .6 | .60 | .58 | .56 | .54 | .52 | .50 | .48 | .46 | .44 | .42 | .40 |
| .7 | .70 | .66 | .62 | .58 | .54 | .50 | .46 | .42 | .38 | .34 | .30 |
| .8 | .80 | .74 | .68 | .62 | .56 | .50 | .44 | .38 | .32 | .26 | .20 |
| .9 | .90 | .82 | .74 | .66 | .58 | .50 | .42 | .34 | .26 | .18 | .10 |
| 1.0 | 1.00 | .90 | .80 | .70 | .60 | .50 | .40 | .30 | .20 | .10 | 0 |

### Explanation of the Table

Table of the values of the cross-over ratios resulting from combinations of different exchange ratios, from 0 to 1, of two pairs of factors. Based on the formula:

$$C = x + y - 2xy$$

Where $x =$ the exchange ratio of one pair,

$y =$ the exchange ratio of the other,

and $x \gtreqless y$.

Outside the square (above and to the left) are the exchange ratios, by tenths, from 0 to 1; within are the cross-over ratios. To find the cross-over ratio resulting from any two exchange ratios, trace the rows and columns of figures from the two exchange ratios till they intersect; thus the cross-over ratio resulting from an exchange ratio in one pair of .6, in the other of .3, is .54.

The table shows directly the limiting values for the cross-over ratios from any two exchange ratios that are not exactly the same as those of the table. Thus:

If the upper left quadrant:

If x or y or both are below the values given in the table, the cross-over ratio is below the value given in the table. Thus if x is below .2 and y is below .3, the cross-over ratio is below .38. If both are below .10, the cross-over ratio is below .18.

If x or y or both are above the values given in the table, the cross-over value is above that given in the table.

In the lower right-hand quadrant:

If $x$ or $y$ or both are above the values in the table, the cross-over value is *below* that given in the table.

If $x$ or $y$ or both are below those in the table, the cross-over value is above that of the table.

In the other two quadrants (upper right and lower left):

If $x$ is smaller and $y$ larger than in the table, the cross-over ratio is above that of the table.

If $x$ is larger and $y$ smaller than in the table, the cross-over value is below that of the table.

Example: $x$ and $y$ given; limits of $C$ required:

$$x = .16,\quad y = .29;\quad C < .38 \text{ and } > .26$$

$$x = .09,\quad y = .08;\quad C < .18 \text{ and } > .0$$

$$x = .13,\quad y = .73;\quad C < .74 \text{ and } > .62$$

$$x = .54,\quad y = .63;\quad C < .50 \text{ and } > .48$$

$C$ given; limits of $x$ and $y$ required:

$$C = .434,\quad x \text{ and } y \text{ both } \leqq .434, \text{ or both } \geqq .566$$

$$C = .021,\quad x \text{ and } y \text{ both } \leqq .021, \text{ or both } \geqq .979$$

$$C = .63;\quad x \leqq .37 \ :\ y \geqq .63$$

$$C = .96;\quad x \leqq .04 \ :\ y \geqq .96$$

$$C = .50;\quad x = .50 \ :\ y = \text{any value from 0 to 1.}$$

The formula for examination is:

$$C = x + y - 2xy$$

(in which $x$ and $y$ are proper fractions).

1. Two exchange ratios, $x$ and $y$, give the same cross-over ratio ($C$) as do their complements, $1 - x$ and $1 - y$. For

$$x + y - 2xy = (1 - x) + (1 - y) - 2(1 - x)(1 - y),$$

as will be seen by performing the operations indicated in the second member of the equation. But this second member is the value of $C$ for exchange ratios $1 - x$ and $1 - y$.

For example, the two exchange ratios .2 and .3 give the same cross-over ratio as do the two exchange ratios .8 and .7; for both cases $C = .38$. This relation is seen in the symmetrical constitution of the table; the cross-over ratio resulting from .1 and .2 is the same as that from .9 and .8; the cross-over ratio resulting from exchange ratios .4 and .7 is the same as that resulting from .6 and .3, etc. The rule holds equally for values not found in the table; thus the cross-over ratio resulting from .011

and .031 is the same as that resulting from .989 and .969.

2. If one of the two exchange ratios is changed to its complement, the cross-over ratio is changed to its complement.

That is, if the cross-over ratio resulting from x and y is C, the cross-over ratio resulting from x and $1-y$, or y and $1-x$ is $1-C$.

For:

$$x+(1-y)-2x(1-y)=1-(x+y-2xy)$$

But the first member of this equation is the cross-over ratio from x and $1-y$, while the second member is 1 minus the cross-over ratio from x and y. The same result is reached if we take y and $1-x$.

Thus, as the table shows, the cross-over ratio resulting from .2 and .3 is .38, so that the cross-over ratio from .2 and .7 is .62, as is likewise the cross-over ratio from .8 and .3 $(.38+.62=1)$. Similarly, the cross-over ratio of .011 and .031 is .0413; hence the cross-over ratio from .011 and .969 is .9587.

3. When the cross-over ratio is less than ½, the exchange ratios x and y are either both greater than ½ or both less than ½; one can not be less than ½, the other greater. That is:

If $C<\frac{1}{2}$ then either $x<\frac{1}{2}$ and $y<\frac{1}{2}$ or $x>\frac{1}{2}$ and $y>\frac{1}{2}$. For let us suppose that $x=\frac{1}{2}-a$ and $y=\frac{1}{2}+b$, in which $a$ and $b$ are any positive quantities. Then $C=x+y-2xy=\frac{1}{2}+2ab$. Therefore x can not be less than ½ and y more than ½.

On the other hand, if $x=\frac{1}{2}-a$ and $y=\frac{1}{2}-b$, or if $x=\frac{1}{2}+a$, $y=\frac{1}{2}+b$; in either case $C=x+y-2xy=\frac{1}{2}-2ab$. So that in these cases the cross over-ratio C is less than ½.

4. Conversely to 3, when the exchange ratios x and y are both less than ½, or when they are both more than ½, the cross-over ratio is less than ½.

That is, when $x<\frac{1}{2}$ and $y<\frac{1}{2}$, or when $x>\frac{1}{2}$ and $y>\frac{1}{2}$; in either case $C<\frac{1}{2}$. This was proved under 3.

5. When the cross-over ratio is greater than ½, one ex-

change ratio is less than ½, the other greater than ½. That is: If $C > ½$, then $x < ½$, $y > ½$. This also was proved under 3.

6. Conversely to 5, when one exchange ratio is less than ½, the other greater than ½, the cross-over ratio is greater than ½. That is: If $x < ½$, $y > ½$, then $C > ½$. This also was proved under 3.

All these relations are evident in the table.

7. When the cross-over ratio is less than ½, the two exchange ratios are either both equal to or less than the cross-over ratio; or both equal to or more than the complement of the cross-over ratio. They can not have any value lying between the cross-over ratio and its complement. That is: When $C < ½$, either x and y each $\leqq C$ or x and y each $\geqq 1 - C$.

This is an extremely important principle, on which the final test of the theory depends. It is proved as follows:

In 3 we saw that if the cross-over ratio is less than ½, either x and y are both less than ½; or both of them are greater than ½.

(*a*) Let us take first the case where x and y are each less than ½. In this case, in the formula $C = x + y - 2xy$, the quantity 2xy is smaller than x, and smaller than y. For since x is less than ½, 2x is less than 1, whence it follows that 2xy is less than y; and the same reasoning shows that 2xy is likewise smaller than x. Hence the formula for C subtracts from the sum of x and y a quantity smaller than y; it therefore leaves a quantity larger than x; and the same reasoning shows that it leaves a quantity larger than y. Only in the limiting case that $x = 0$ does $y = C$.

(*b*) Take next the other possible case, in which x and y are both greater than ½. In this case $1 - x$ and $1 - y$ are both less than ½. Thence it follows (by the reasoning just employed) that

$$(1 - x) + (1 - y) - 2(1 - x)(1 - y)$$

is greater than $1 - x$ and greater than $1 - y$. But, as was seen in (1),

$$(1-x)+(1-y)-2(1-x)(1-y)=x+y-2xy\equiv C$$

So that in this case $C>1-x$ and $C>1-y$.

Thus the fraction C is nearer to 1 than the fraction $1-x$. If therefore we subtract the fraction C from 1, it will leave a smaller number than if we subtract the smaller fraction $1-x$ from 1. That is: $1-C<x$.

And in the same way it can be shown that $1-C<y$. Only in the limiting case that $y=1$ does $x=1-C$.

The general principle in this section can be expressed as follows:

When the cross-over ratio is less than ½, the two exchange ratios, x and y, either both differ from 0 by less than the cross-over ratio, or both differ from 1 by less than the cross-over ratio.

This relation is well seen in the table. For example, for the cross-over ratio .38 the two exchange ratios are either .3 and .2 (both less than .38), or they are .8 and .7 (both greater than .62, the complement of .38).

8. Conversely to 7:

If both exchange ratios, x and y, are less than ½, both are equal to or less than the cross-over ratio.

If both exchange ratios, x and y, are greater than ½, both are equal to or greater than the complement $(1-C)$ of the cross-over ratio.

9. When the cross-over ratio C is above ½, one of the exchange ratios (x) is equal to or less than the complement of the cross-over ratio $(1-C)$, while the other (y) is equal to or more than the cross-over ratio (C).

Or otherwise expressed:

When the cross-over ratio is above ½, one of the exchange ratios (x) differs from 1 by an amount equal to or more than the cross-over ratio, while the other (y) differs from 0 by an amount equal to or more than the cross-over ratio. That is, when $C>\frac{1}{2}$, $1-x \geqq C$, $y \leqq C$, or $x \leqq 1-C$, $y \geqq C$.

This can be proved by methods similar to those employed in 7.

10. Conversely to 9:

When one exchange ratio (x) is less than ½, the other (y) greater than ½, the cross-over ratio can not be greater than y nor than 1 — x:

If $x < \frac{1}{2}$ and $y > \frac{1}{2}$, $C \leqq y$, $C \leqq 1 - x$.

All these relations 1 to 10 are clearly illustrated in the table.

III

These relations being established, we may turn to a test of the theory by the facts. Do the cross-over ratios experimentally established in such an organism as *Drosophila* show the relations which this theory requires?

Some of the cross-over ratios determined by Morgan and his associates for various pairs of factors in the sex chromosome of *Drosophila* are the following (taken from the list given by Morgan and Bridges, 1916, page 84).

| No. of cases examined | Factors | Cross-over Ratio |
|---|---|---|
| 81,299 | Yellow-White | .011 |
| 6,461 | White-Rudimentary | .424 |
| 1,456 | Rudimentary-Forked | .014 |
| 2,563 | Yellow-Rudimentary | .429 |
| 13,271 | Yellow-Vermilion | .345 |
| 10,155 | Vermilion-Miniature | .031 |
| 12,786 | Miniature-Rudimentary | .179 |
| 626 | Yellow-Bar | .479 |
| 8,768 | Bar-Fused | .025 |
| 5,955 | White-Bar | .436 |

The cross-over ratio for yellow-white, as shown above, is .011. Therefore, on the theory with which we are dealing, according to principle 7, given above, the exchange ratio for yellow is either equal to or less than .011; or else it is equal to or greater than .989. It can not lie between these numbers. (The same is of course true for the factor white.)

Further, the cross-over value for vermilion-miniature is .031, whence it follows from 7 that the exchange ratio for vermilion is equal to or less than .031, or it is equal to or greater than .969. It can not lie between these values.

What then are the possible cross-over values for yellow-vermilion?

If we give both these factors their maximum exchange ratios lying below ½ (that is .011 and .031), or their minimum exchange ratios lying above ½ (that is, .989 and .969), then work out the cross-over ratio by the formula: $C = x + y - 2xy$, we obtain the same result; the cross-over ratio yielded is .041. But as our list shows, this is less than ⅛ the actual value, which is .345. If we decrease the two low ratios, or increase the two high ones (which are the only changes the theory allows), the cross-over ratio becomes still less and still farther from the reality.

Suppose then we try giving one factor its possible exchange ratio above ½, the other its possible exchange ratio below ½. But we know already, by 6, that this will give us a cross-over ratio above .50, whereas the actual ratio is but .345. If we actually work out the ratios, we find that the minimum cross-over ratio that we can obtain in this way is .959, in place of the actual .345.

Thus on this theory the only cross-over ratios that the pair yellow-vermilion can have, consistently with the values of the cross-over ratios yellow-white and vermilion-miniature, either lie below .041 or above .959; yellow-vermilion can not have a cross-over ratio lying between these values. Yet the actual value (from the study of 13,271 cases) is .345.

This example is typical. We shall come to the same kind of a result if we examine many other cross-over ratios in *Drosophila*. For example, we find that yellow-white yield the ratio .011; rudimentary-forked the ratio .014. It follows from this that the cross-over ratio for white-rudimentary either lies below .025 or above .975; on this theory it can not lie between these values. Yet its actual value is .424—very near the middle of the region of values which the theory does not permit it to hold. And similarly for other pairs. It is a necessary consequence of this theory that if two factors each give with any other factors extreme cross-over ratios (very

high or very low), they can not together give cross-over ratios of the more intermediate values. For example (as our table shows), if two factor pairs each give, with any other, cross-over ratios below .10, they can not give together a cross-over ratio lying anywhere between .18 and .84. If the two pairs each yield any cross-over ratios lying below .20, they can not give together a cross-over ratio lying between .32 and .68. These and many similar relations, illustrated in the table, are inherent in the theory we are considering, but are completely opposed to what is found in nature.

## IV

These facts completely refute any theory which holds that the observed constant cross-over ratios between pairs of factors are the result of constant exchange ratios between the two members of a given pair—exchange ratios that are characteristically diverse for the different pairs (such theories as that outlined by Goldschmidt, 1917). The refutation is independent of the question of the nature of the forces involved; whatever the forces, if they give constant average exchange ratios for each pair, the results are bound to be inconsistent with the observed cross-over ratios. No theory will hold that does not provide for diverse relations between the different factors in the same chromosome, such that some tend to cling together more frequently than others.

Possibly some elements of the theory that diverse exchange ratios are characteristic for different pairs might be retained, if there be added provision for modification of the exchange ratio in a given pair, depending on whether or not exchange occurs in some other pair. It might be held, for example, that $A$ and $a$ are more likely to exchange if in the same cell $B$ and $b$ have exchanged; or the reverse. This would give a theory of mixed type, which added to the forces regulating the exchange between two members of a pair, other forces causing two given pairs to tend to do the same thing, or the opposite

thing. The "variable force" theory would therein approach the chiasmatype theory, in which the diverse relations between the factors belonging to different pairs are the primary, if not the exclusive, elements considered.

As theories of other type become successively modified so as to take into account the known facts: the fact that the chromosome actually is a linear aggregate; the fact that the two chromosomes while in this linear condition pair and intertwine; the fact that cross-overs occur only at the period when this occurs; the fact that two recessive allelomorphs when mated do not produce normals, while two recessives not allelomorphs do; the fact that after two factors, A and B, are found to hold together in one generation, if we mate their cross-overs *A–b* and *a–B*, we now find that it is *A* and *b*, not A and B that tend to hold together (Bridges, 1917); the fact that when a given factor is lost from a chromosome, others that have low cross-over ratios with that factor are also lost (Bridges, 1917*a*);—when the modifications required for bringing these facts into relation with each other and with others are introduced, it appears that the resulting theory will come more and more to resemble the chiasmatype theory. No theory is adequate that does not include and bring into relation the facts just mentioned, for a correct theory is nothing but a presentation of the facts in their correct (verifiable) relations.

PAPERS CITED

Bridges, C. B.
1917. An Intrinsic Difficulty for the Variable Force Hypothesis of Crossing Over. AMERICAN NATURALIST, 51: 370–373.

Bridges, C. B.
1917*a*. Deficiency. *Genetics*, 2: 445–465.

Goldschmidt, R.
1917. Crossing Over ohne Chiasmatypie? *Genetics*, 2: 82–95.

Morgan, T. H., and Bridges, C. B.
1916. Sex-linked Inheritance in *Drosophila*. Publication No. 237, Carnegie Institution of Washington. 87 pp.

# SHORTER ARTICLES AND DISCUSSION

## NOTE ON THE COLORATION OF PLANES MINUTUS[1]

It is well known that the coloration of the grapsoid crab *Planes minutus*, a constant member of the Sargassum fauna, is "homochromic" to a high degree, not only as to tint and mottling, but also in the frequent occurrence of a blotch of pale yellowish or blank white upon the carapace; this has generally been supposed to be a mimicking of the white patches of encrusting bryozoa and *Spirorbis* tubes, which commonly infest the Sargassum.[2] Experiments made to discover the extent of possible color changes in the adult *Planes* when it is placed over variously pigmented artificial bottoms have led to no result, other than to show—conformably with what is known for some other crustacea possessing a dense body pigmentation, as contrasted with a relatively scanty supply of well-scattered chromatophores—that the power of color adaptation is decidedly limited. It is, therefore, of interest to make record of an instance in which pronounced color adaptation of *Planes* had occurred in nature.

In January, 1916, after a rather severe gale, there was found stranded upon one of the reef "heads" at Bermuda a large "Spanish cedar" tree. It is certain that the tree had been in the sea for some time, as the surface layer was thickly populated by *Teredo* and boring amphipods. The trunk, the stumps of the roots and the submerged branches of the tree were covered with a forest of barnacles, *Lepas anatifera*, from among whose smoky-brown erectile peduncles were obtained a vast number of adult *Planes minutus* that were adhering to the more or less honeycombed parts of the exposed bark and wood. Without exception the crabs were deep brownish-red, save for the frequently occurring dorsal white patch. This pigmentation harmonized precisely in general tint with the mahogany-colored surface of the cedar tree.

The interest of this case lies in its demonstration that these crabs—prominent members of that specialized gulf-weed fauna which has been urged as part of an argument for the antiquity

[1] Contributions from the Bermuda Biological Station for Research, No. 84.

[2] *Cf.* Verrill, 1908, Pl. XIII; Murray and Hjort, 1912, p. 671, Pl. VI.

of the floating beds of Sargassum (Collins, 1917), probably for generations experiencing no other habitat than the gulf-weed—having yet retained a considerable capacity of color adaptation. Among Sargassum the hues of *Planes* vary considerably,[3] but the color of the present specimens was very much darker and redder than that of any I have seen described. The color agreement could hardly have resulted from a general staining of the crabs following ingestion of pigment derived from the tree, as the characteristic white blotch upon the dorsum was fully as well, if not somewhat more, developed in many of these specimens, than in the common ones living upon gulf-weed. Spectroscopic examination of alcoholic extracts of these crabs showed that the pigment was not detectably different from that of *Planes* taken on Sargassum. Whether the white patch represents in this instance an inherited tendency to lack of pigment on that area, or is rather to be regarded as (in addition) a mimicking of the white valves of the accompanying Lepads, is a question; the conspicuous development of the white shield, its large size and precise outline in more than 50 per cent. of the individuals, suggests the possibility of the latter alternative.

Presumably the floating cedar tree was invaded by *Planes* larvæ, which developed upon this dark reddish-brown substratum, and, like Hippolyte in the experiments of Gamble and Keeble (1900), produced there a pigmentation of corresponding appearance. In this way a coloration might be acquired which the crabs probably could not, at least quickly, have accomplished by adaptive color change in the adult state. No color changes were detected when these dark crabs were kept for six days upon Sargassum, in bright light.

## REFERENCES

Collins, F. S.
1917. The Sargasso Sea. *Rhodora*, Vol. 19, pp. 77–84.

Gamble, F. W., and Keeble, F. W.
1900. *Hippolyte varians:* A Study in Color-Change. *Quart. Jour. Micros. Sci.*, Vol. 43, pp. 589–698.

Murray, J., and Hjort, J.
1912. The Depths of the Ocean. London, 8vo., xx + 821 pp.

Verrill, A. E.
1908. Decapod Crustacea of Bermuda, I: Brachyura and Anomura. *Trans. Conn. Acad. Arts and Sci.*, Vol. 13, pp. 299–474.

AGAR'S ISLAND,
BERMUDA

W. J. CROZIER.

[3] *Cf.* Murray and Hjort, 1912, Pl. VI.

## THREE MUTATIONS IN PREVIOUSLY KNOWN LOCI

THREE mutations is the sex-chromosome have occurred in my cultures of *Drosophila melanogaster* (*ampelophila*). Two were reappearances of genes already known, namely, white and rudimentary; the third was the appearance of a new gene at the white locus and has been named coral, symbol $w^{co}$. In each case it is clear that the changes occurred in the wild type gene of a maternal chromosome. The evidence also indicates that the new gene arose relatively late in the history of the egg in each case, whereas if the mutation had occurred in the early oogonial stages several individuals with the new gene should have appeared. In cases where such information is known, it seems worth recording since it will make possible a later consideration of the relative stability of genes by a summing up of the frequency of mutations in the different loci.

As has been pointed out by Muller[1] recessive genes might exist for a long time before making an appearance, in case they were closely linked to a lethal. The character produced by the gene would ultimately be allowed to appear as the result of a cross over which would separate the gene and the lethal from the same chromosome. Previous to the time of crossing-over the character produced by the gene would never be seen, since all individuals pure for it would also be pure for the lethal and not survive. The gene could be indefinitely transmitted along with the lethal through heterozygous individuals. I mention this point because it is necessary in establishing the time of origin of a mutation to consider whether its appearance may be due merely to its recent separation from a lethal, which had obscured it. The three mutations dealt with here could not have been masked by a lethal because they were in the X-chromosome, and the presence of a lethal would have been apparent, as it would have produced a lethal sex ratio. No such lethal ratio has been found in connection with any of the three mutants either before or since their appearance. In these cases, then, it is safe to assume that the appearance of the first mutant marks the time of the mutation. If the mutation had occurred in earlier generations, several individuals bearing the character would have appeared instead of one.

In the case of the reappearance of a character, careful consideration must be given to the possibility of contamination, as has

[1] *Proc. Nat. Acad. Sci.*, Vol. 3.

been pointed out by Morgan and Plough.[2] This possibility has been taken into account and is discussed with reference to the appearance of each gene in that particular section.

### Origin and Description of Coral

Coral arose in a mating of an eosin miniature bar-eyed male to a forked female with normal eyes. This female was a "secondary exception" from an XXY mother which had had no sex-linked eye color in her pedigree. Among 279 offspring that were of the expected classes and showed no lethal sex ratio, there was found about the middle of the count one heterozygous bar female which seemed to be "exceptionally" dark eosin. An eosin eye color in a female would be impossible to account for, since to be a female she must have obtained one of the mother's chromosomes, both of which carried normal red factors, as well as receiving the eosin bar chromosome of the father. A mating to one of her red-eyed brothers showed at once that the supposed eosin female was actually heterozygous for eosin and for a new allelomorph (coral) as she gave two kinds of sons, eosin and coral, while the daughters were eosin and the compound eosin-coral. The eosin-coral females are darker than pure eosin females and the original female was of this nature.

Coral is the seventh mutant allelomorph to be found in the white locus and counting the wild type gene forms with them a system of eight allelomorphs. In the order of their discovery these are: red, white, eosin, cherry, blood, tinged, buff and coral. Coral does not show bi-colorism, but is the same for males and females. It is similar to the color of very dark coral. It is darker than all the other members of this series with the possible exception of blood which according to the description of Hyde in his discussion of blood[3] shows a considerable variation of color according to cultural conditions. The color of coral is very close to the darker shades of blood, but is much darker than the lighter shades and does not show any such variations in range of color. Coral is distinctly darker than cherry and the other lighter members of this series. Coral is a dull color and does have the brightness of color of the wild stock, neither does it show the fleck in the eye.

The original coral female was re-mated to a white male from stock and behaved genetically, as would be expected on the as-

[2] Amer. Nat., Vol. 49.

[3] *Genetics*, 1, November, 1916.

sumption that coral was a member of the white allelomorphic series. The heterozygous white-coral compound in the female is intermediate in color between the two pure stocks. Coral is recessive to red. A coral male crossed to a yellow-white female gave all yellow-white sons and the intermediate (compound) white-coral daughters. Evidently the mutation took place in the wild-type gene of the mother, since it is that gene which did not occur in the daughter while the eosin gene of the father is retained. It also occurred near the maturation divisions as only one individual of the kind appeared. If the change had occurred in the early stages of the egg, it would probably have resulted in several of the offspring showing the new character.

### Reappearance of White

In a cross of a bar male to a red-eyed female, which produced 251 offspring without a lethal sex ratio, one male was obtained which was white, although there was no white in the pedigree of either parent. This fly was found in one of the last counts of the bottle and had the appearance of being a young fly. Counts were made from the bottle every two days. Since I had no cultures going at that time which contained white and had had no white flies in my etherizing bottle previously, the fly can not be accounted for by assuming that it had remained in the etherizing bottle from a previous count of another bottle. It is highly probable, though not absolutely certain from these considerations that this white male was not due to contamination, but rather to a mutation in the wild type gene of a maternal chromosome. We may be sure that this change took place in the maternal chromosome rather than in that of the father, since males always receive their one X-chromosome from the mother except in relatively rare cases of non-disjunction, and in this case the male would have been bar.

In appearance the new white is not distinguishable from the white of the original stock and is quite without color in both males and females. Dr. A. H. Sturtevant has been testing the effect of various concentrations of alcohol in extracting color from the eyes of flies which are members of this multiple allelomorphic series and kindly added this new white to the material which he tested. He reported that the new white is acted upon exactly as is the original white. Genetic results showed the new white to behave as an allelomorph of the old. The new white male was crossed to a red sister and the offspring were all red.

The $F_2$ generation gave females all red and the males in equal classes of red and white, which is the genetic behavior expected for a sex-linked gene. To test whether this white was in the same locus as the old white, a white male of this stock was crossed to a yellow-white female from the original stock. The sons were yellow white and the daughters were white, not yellow, since yellow is recessive and was not carried by the father. No difference could be observed in eye color between either sex of the new white, or the daughters compounded from the two whites, and the males and females of the original white. It seems reasonable to conclude then that the white gene has reappeared by a second mutation from the red gene.

### Second Origin of Gene for Rudimentary Wing

There appeared in a cross of an eosin miniature male to a broad, vermilion, forked female (both from stock cultures, all characters mentioned being sex linked) one son which was vermilion, forked like the mother, but which also had shortened wings. This wing character was later shown to be rudimentary. Crossovers in later generations showed that the maternal gene for broad was also present, but its effect was obscured by the rudimentary in all cases where both occurred together. This male so obtained and bearing genes for broad, vermilion, rudimentary and forked was outcrossed to a virgin wild type female to test whether the new character was of a genetic nature. The $F_1$ flies were normal in all respects. One pair of these produced 117 sons which were classified with respect to the characters vermilion, rudimentary and forked, while no attention was paid to broad, which did show in certain crossovers where it was separated from rudimentary. Out of 117 males, 3 were crossovers between rudimentary and forked, which gave a percentage of crossing-over of 2.6, whereas the value given by Morgan and Bridges[4] is 1.4 on the basis of a much larger number of flies. There were 27 crossovers between rudimentary and vermilion, which is a percentage of 22.2, while the above authors put it at 24.1. The nature of the crossovers obtained showed that the gene for the wing character was between vermilion and forked, which agrees with the assumption that it is a new appearance of rudimentary. The crossover values obtained are sufficiently near to expectation to justify this assumption in view of the small number of flies. Crosses were made to the stock rudimen-

[4] Carnegie Pub. No. 237, 1916.

tary to make sure that the new gene was at the rudimentary locus. Since homozygous rudimentary females show a high degree of sterility, the rudimentary stock is kept by crossing it to forked and using normal-winged females that are heterozygous for both rudimentary and for forked. One of the new rudimentary males was crossed to such a heterozygous female and the new rudimentary was shown to be an allelomorph of the old, as both rudimentary sons and daughters were obtained in practically equal numbers. The new rudimentary stock resembled the old as regards the sterility of the homozygous females. Miss C. J. Lynch in this laboratory tested several and reported that they showed the same high degree of sterility. Since the new character has the same appearance as old rudimentary, this seems to be merely the reappearance of that gene.

In this case it is clear that the change occurred in one of the maternal sex-chromosomes which already carried three sex-linked genes. The linkage relations of the new gene to these maternal genes make its origin in the maternal chromosome certain. Moreover, the male could have received his sex-chromosome only from his mother, as otherwise he would have been an XO male and would have been sterile.[5] The fly could not be accounted for on the assumption of contamination, as there are no flies of that particular constitution in the laboratory. The mutation was from the normal gene at the rudimentary locus. The appearance of only one individual indicates that the change occurred late in the history of the egg.

## SUMMARY

1. Two mutations have occurred at the white locus in the normal red gene, giving rise to a reappearance of white and to a new gene which produces an eye color called coral.

2. Coral is the eighth member of the multiple allelomorph series at the white locus.

3. Rudimentary reappeared as a change from the normal gene at that locus in a maternal chromosome.

## LITERATURE CITED

Bridges, C. B.
1916. Non-disjunction as Proof of the Chromosome Theory of Heredity. *Genetics*, I, 1–52, 107–163.

Hyde, Roscoe R.
1916. Two New Members of a Sex-linked Multiple Allelomorph System. *Genetics*, I, 535–580.

[5] Bridges, *Genetics*, II, 1916.

Morgan, T. H., and Bridges, C. B.
1916. Sex-linked Inheritance in *Drosophila*. Carnegie Publication No. 237.

Morgan and Plough.
1915. Appearance of Known Mutations in other Mutant Stocks. Amer. Nat., Vol. XLIX.

Muller, H. J.
1917. An *Œnothera*-like case in *Drosophila*. *Proc. Nat. Acad. Sci.*, Vol. 3.

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## EVIDENCE FROM INSULAR FLORAS AS TO THE METHOD OF EVOLUTION

Evidence as to the rôle which hybridization plays in evolutionary change may be obtained from various insular floras by a comparative study of the history of those plant types in them which are prevailingly self-fertilized and those which are prevailingly cross-fertilized, both as to the rapidity with which new local species are produced and as to the frequency with which old species disappear. With these points in view, analyses have been made of the vascular plants in the floras of eight islands or island groups: Ceylon, Mauritius, Socotra, New Zealand, Hawaii, Galapagos, Juan Fernandez and St. Helena.[1] In all these there is a conspicuous, often predominant, element in the flora which is strictly local or endemic, indicating that each island has been the theater of considerable evolutionary change.

Information is necessarily lacking as to the method of fertilization of most of the species, but our general knowledge of the reproduction of the higher plants allows us to divide them into three main types. The dicotyledons and petaliferous monocotyledons, possessing floral organs which in the great majority of cases are attractive to insects, are doubtless prevailingly cross-pollinated. In the glumaceous monocotyledons, on the other hand (chiefly Gramineæ, Cyperaceæ and Juncaceæ), the floral organs are not so constructed as to favor cross-pollination, and it will probably be agreed that crossing is much less common

[*] These analyses are based on the following authorities: Trimen, Handbook of the Flora of Ceylon; Baker, Flora of Mauritius and the Seychelles; Balfour, Botany of Socotra; Cheeseman, Manual of the New Zealand Flora; Hillebrand, Flora of the Hawaiian Islands; Stewart, Botany of the Galapagos Islands; Johow, Flora de las Islas de Juan Fernandez; Melliss, St. Helena; and Hemsley, Report on the "Challenger" Expedition: Botany.

among them than in the petaliferous types. Finally, in the vascular cryptogams, the very frequent occurrence of bisexual gametophytes seems to insure a still greater prevalence of self-fertilization.

The vascular flora of each island was divided into these three groups which were studied comparatively. Determination was first made as to the percentage of local or endemic species in each group. This degree of endemism provides us with a rough measure of the extent to which new forms have been developed on the island, and thus allows us to compare the rapidity of evolution in one floral group with that in the others.[2] In the following table are set forth the percentage of endemic species in each of the three main groups which we have mentioned, and for each of the islands:

TABLE I

PERCENTAGE OF ENDEMIC SPECIES IN VARIOUS FLORAL ELEMENTS

| | Ceylon | Mauritius | Socotra | New Zealand | Hawaii | Galapagos | Juan Fernandez | St. Helena |
|---|---|---|---|---|---|---|---|---|
| Dicotyledons and Petaliferous Monocotyledons ..... Average, 65% | 35% | 55% | 42% | 84% | 84% | 50% | 73% | 100% |
| Glumaceous Monocotyledons ..... Average, 38% | 11 | 14 | 9 | 56 | 60 | 30 | 37 | 87 |
| Vascular Cryptogams ..... Average, 23% | 9 | 20 | 10 | 30 | 51 | 2 | 18 | 44 |

It is evident that the proportion of endemic species is much higher among those types which we have reason to believe are prevailingly crossed than among those which are prevailingly selfed, being highest among dicotyledons, lower among glumaceous monocotyledons and lowest among vascular cryptogams. The same fact appears among genera, for 95 per cent. of the endemic genera of these islands belong to petaliferous types and only 5 per cent. to the glumaceous monocotyledons and vascular cryptogams. These facts all point to the importance of hybridization as a factor in the production of new species.

The other aspect of evolutionary change, namely the disap-

[1] Of course not all the endemic forms can be regarded as of local origin, since certain of them may be isolated relicts of types formerly more widely spread. The proportion of these, however, which have not subsequently undergone specific change, and thus developed true local types, is probably small.

pearance of species, seems also to be influenced by the method of fertilization. Many of the genera which are themselves not endemic on any island are nevertheless represented there now *only* by endemic species. In such cases it seems clear that the first representative of the genus to invade the island has since disappeared there entirely and been replaced by local species. Table II gives the percentage of such genera (not endemic but represented only by endemic species) for each of the three plant types which we have discussed and for all the islands.

TABLE II

PERCENTAGE OF THE NON-ENDEMIC GENERA WHICH ARE REPRESENTED ONLY BY ENDEMIC SPECIES

| | Ceylon | Mauritius | Socotra | New Zealand | Hawaii | Galapagos | Juan Fernandez | St. Helena |
|---|---|---|---|---|---|---|---|---|
| Dicotyledons and petaliferous monocotyledons ........ Average, 42 % | 9% | 28% | 29% | 44% | 57% | 16% | 52% | 100% |
| Glumaceous monocotyledons ........ Average, 26 % | 2 | 11 | 12 | 10 | 40 | 11 | 38 | 83 |
| Vascular cryptogams ........ Average, 10.5 % | 3 | 0 | 0 | 20 | 18 | 0 | 19 | 25 |

It is evident that genera in which the "original species" has become extinct are proportionally commonest among dicotyledons, less common among glumaceous monocotyledons and rare among vascular cryptogams, thus suggesting that hybridization has resulted in the "swamping out" of the early forms. If local adaptation and natural selection alone were at work, it is hard to see why extinction should not be equally common in all these groups. The facts point to the importance of hybridization in completely altering specific type when a group of individuals have been isolated from the main body of the species.

Against the soundness of these conclusions several points may be urged. Vascular cryptogams are perhaps inherently less variable and quick to produce new species than flowering plants. It may be, too, that cross-fertilization is much more common among them than is generally believed. Whether the recognized "species" among these plants is the equivalent of the "species" among angiosperms, or is a much more inclusive group, is also a matter of doubt. These points can not well be brought against the glumaceous monocotyledons, however, as contrasted with the petaliferous types. Whatever its interpretation, the fact seems

clear that among dicotyledons and petaliferous monocotyledons new types are produced and old types lost much more quickly than anywhere else in vascular plants, a fact which in the light of our knowledge of methods of reproduction certainly supports the view that hybridization has been a powerful factor in evolutionary change.

SUMMARY

Evidence from a comparative study of endemism in various elements of certain insular floras tends to show that among cross-fertilized types new species are developed more rapidly and old ones lost more frequently than among self-fertilized types, thus emphasizing the importance of hybridization as a factor in evolutionary change.

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## A LAND PLANARIAN FOUND AT BERMUDA[1]

IN 1902 Professor Verrill recorded ("The Bermuda Islands," p. 436, Fig. 237), that there had been reported to him the finding at Bermuda of a "worm" which appeared to be a land planarian. With the possible exception of this worm, which may have been a *Bipalium,* no land planarians have been seen at Bermuda. While collecting earthworms, in September, 1917, I obtained among moist decaying leaves in a "fertilizer pit" at Point Shares, Pembroke Parish, a single specimen of a flatworm which seems to be a species of *Geoplana.* The "pit" was in use as a dumping ground for garden refuse, and since no land planarians appear to be native to Bermuda, the worm may have been introduced in company with plants. It was 50 mm. long and 2 mm. wide, pale greenish blue on the ventral surface,—which bore a rather small oral sucker in the usual position,—the ground color of the dorsal surface being a deeper shade of the same greenish blue, but marked with two deep blue or black longitudinal stripes running the whole length of the animal. Two well-developed pigment spots were present, one on either lateral margin of the anterior end. It is not impossible that this species might become permanently colonized at Bermuda (although no other specimens have been found), and this note may therefore be of use in fixing the date of its earliest observed appearance.

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AGAR'S ISLAND, BERMUDA

[1] Contributions from the Bermuda Biological Station for Research, No. 85.